# ECOLOGY AND BREEDING BIOLOGY OF THE SCARLET MACAW (*Ara macao*) IN THE USUMACINTA DRAINAGE BASIN OF MEXICO AND GUATEMALA

By

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# ECOLOGY AND BREEDING BIOLOGY OF THE SCARLET MACAW (*Ara macao*) IN THE USUMACINTA DRAINAGE BASIN OF MEXICO AND GUATEMALA

By

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The Scarlet Macaw (Ara macao) is one of the most endangered species of neotropical birds in the northern Central America region. Though once widespread, the species now survives in only two small populations in México. One of these populations was studied in the Usumacinta drainage basin of México and Guatemala. The population in the area is very small, causing the species to be classified as being on the verge of extinction.

I compared the macaw groups in two main habitats, continuous and disturbed forests, in order to investigate the range of environmental conditions affecting the species' distribution. I compared data from walking transects versus boat river surveys and did not detect any significant differences in macaw abundances in either continuous or disturbed forests. These findings suggest that the species has similar behavior in both habitat types, which may facilitate conservation management.

The population of Scarlet Macaws in the Usumacinta drainage basin has a chance for survival. If all sub-populations in the north Central America region (México, Guatemala, Belize) were managed as a metapopulation, which may include reintroduction, translocation and/or managed dispersal of individuals among its sub-populations, there is a high probability of its long-term survival in the wild.

# CHAPTER 1
# GENERAL INTRODUCTION

## Description of the Study

In this dissertation I examine the ecology and conservation biology of a Scarlet Macaw (Ara macao; Class Aves, Order Psittaciformes) population in the Mayan riparian forests of Mexico and Guatemala. I consider issues relevant to population ecology, breeding biology, foraging behavior, conservation biology, landscape ecology, management of protected areas, and habitat use using remote sensing techniques. With these techniques I present a detailed characterization of one of the largest remaining areas covered with tropical evergreen forest in North America. I also examine issues related to the current conservation and management efforts in both Montes Azules and Lacantún Biosphere Reserves and the Yaxchilán Natural Park, all in the Selva Lacandona region of Chiapas, México, as well as in a portion of the south-west lands of both the Sierra del Lacandón National Park and the buffer area of the Maya Biosphere Reserve in the Department of Petén, Guatemala.

The scarcity of biological information available on Scarlet Macaws living in the wild necessarily makes this study exploratory in nature. When information was sufficient, I generated and tested comparative hypotheses. I predominantly used an inductive approach, but not exclusively, in Chapters 3, 4, and 5.

## Aims of the Study

The world today is being affected by human activities at a faster rate, yielding more extensive impacts than ever before in history. Current remnant wildlife populations, habitats, and ecosystems are being fragmented, reduced, polluted, and exploited. Several authors have estimated that between 5 and 20% of some groups of living species will be threatened with extinction in the foreseeable future (Shaffer 1987, Kaufman 1993, WRI 1996). Ehrlich (1988) suggested two main types of species threats: "direct endangerment", which is the deliberate overexploitation of wildlife by human beings, and "obscure endangerment", which includes the loss of genetic diversity within a population and the fragmentation and destruction of species habitats. It has been argued that one of the major challenges for conservation biology is to alleviate the long-term consequences of population and habitat fragmentation (Saunders et al. 1987). In this dissertation I attempt to address this challenge based on the conservation biology principles advanced by Soulé (1986).

The main focus of this study is the ecology and conservation biology of the Scarlet Macaw in the northern neotropics. I conducted field work during August-December 1989, January-December 1990, and January-May 1993 along the Usumacinta drainage basin of México and Guatemala. The region is a landscape mosaic of continuous tropical forest and anthropogenic disturbed habitats that includes numerous forest fragments of various sizes, shapes, and patterns of isolation and extent of edges.

## Goals and Objectives

The goals of the present dissertation are to (1) synthesize the natural history of the Scarlet Macaw found on the Usumacinta drainage basin of México and Guatemala; (2) place this information in the context of the Scarlet Macaw breeding cycle; (3) compare this information in the current setting of ecological correlates and habitat change in a complex and dynamic tropical landscape; and (4) determine which characteristics of this species are important in establishing management guidelines and conservation strategies for the species and its habitat.

The dissertation is divided in six chapters. In Chapter 1 (this chapter) I present a description of the study. In Chapter 2 I present the background for the subsequent chapters of the dissertation. I include a review of the natural history literature of the Scarlet Macaw in other Neotropical regions. I present a review of the available literature related to the species' historical distribution in México and to the biology of this species in the wild. In Chapter 3, I examine the sampling detectability differences by walking and boating along transect surveys in continuous and disturbed forests. In Chapter 4 I examine nesting sites, nesting habitat, and nesting cavity availability of Scarlet Macaws. In Chapter 5 I focus on the breeding biology and nesting cycle of the Scarlet Macaw in two main habitat types by comparing the number of nests and nest success in continuous versus disturbed forests. Finally, in Chapter 6, I summarize and discuss the dissertation's major results.

# CHAPTER 2
# THE SCARLET MACAW: NATURAL HISTORY AND CONSERVATION

## Introduction

The Psittaciformes represent the third-largest non-passerine avian order thought to have evolved from an arboreal ancestor. The evidences supporting this origin includes zygodactylous feet, a hooked bill commonly used for tripodal progression, cavity nesting, white egg shells, and a diet concentrating on canopy fruits (Smith 1975, Forshaw 1989, Sibley and Ahlquist 1991). The order probably originated in the Australasian region with an old and independent evolutionary history (Homberger 1991). This order is clearly defined and has no marginal taxa that could suggest phylogenetic affinities to other avian orders. The Psittaciform lineage has demonstrated a remarkable resilience in adapting to widely differing ecological conditions while at the same time retaining a set of ancestral psittaciform characters.

Psittaciformes show a number of common characteristics: presence of a hooked bill; prehensile feet; zygodactil feet; five intestinal loopings; lack of caeca; oil gland tufted or absent; hinged, weak or absent furcula; upper mandible adapted for tripodal progression; tongue with prominent musculature and hyoid bones used as thigmotactile organ (i.e., continuous response of an organ with solid surfaces); highly flexible attachment of the upper jaw with the cranium; diastic wing; sexually monomorphic species; and altricial young that are fed by the parent holding the chick's bill in its own (Ridgway 1916, Smith 1975, Homberger 1991).

Information on the breeding biology, nutritional physiology, health, and diseases has been extensively documented for captive psittacines (Greene 1884-1887, Tavistock 1929, Stoodley and Stoodley 1983, Takeshita et al. 1986, Jordan 1989, Kollias 1989, Aschenborn 1990, Low 1990, Abramson 1991, Schubot et al. 1992, Abramson et al. 1995), whereas information with wild macaws is limited (Saunders 1974; Ridgely 1982; Saunders et al. 1985; Saunders 1986; Snyder et al. 1987; Forshaw 1989; Gnam 1990, 1991; Rowley 1994; Munn 1991; Waltman and Beissinger 1992, Emison et al. 1994; Enkerlin-Hoeflich 1994).

In the Neotropics, psittacines (including macaws, amazons, parrots, parakeets, parrotlets, and conures; hereafter usually referred to as parrots) show the highest levels of endangerment of any avian family (Wege and Long 1995). Forty-two of the 140 species (30%) of Neotropical psittacines are in danger of extinction (Ridgely 1981; Forshaw 1989; Collar and Juniper 1992; Collar et al. 1992, 1994; Wege and Long 1995). This is due to several factors such as exploitation for pet trade (Iñigo-Elias and Ramos 1991), habitat loss (Yamashita and Valle 1993) and hunting (Redford and Robinson 1987). An estimated 76 to 86 species of Neotropical psittacines are sold in the international wild-caught bird trade (Allen and Johnson 1991, CWS 1994).

The two species of macaws extant in México, the Scarlet Macaw (*Ara macao*) and Military Macaw (*A. militaris*), have declined dramatically during the last 100 years. Ridgely (1982) cautioned that the Scarlet Macaw "..has in fact decreased precipitously over the last half-century; probably no other Mexican bird has undergone such a drastic decline." Recently (Howell and Webb 1995) suggested that the Scarlet Macaw population could be extirpated "completely from [the] region [México and north Central America] within a few years" (Howell and Webb 1995).

Studies of the population biology and dynamics of wildlife have been shown to be particularly useful in understanding the regulation of psittacine population fluctuations (Snyder *et al*. 1987). Moreover, such studies provide crucial information in designing management strategies for endangered species and conservation of ecosystems (Soulé 1986, Soulé and Kohm 1989, Clark *et*. *al*. 1994). Thus, the main goal of this research has been to gather long and short-term information to conserve the Scarlet Macaw and its habitat in México and Central America.

## Phylogeny and Classification

### Macaws In The Neotropics

There are 139 extant psittacine species in the Neotropics, 66% belong to only six genera including Ara (Ridgway 1916, Forshaw 1989). Macaws are one of the most familiar groups of Neotropical parrots. It is not clear how many extant genera and species of psittacidae birds belong to the macaw group. In this study I follow the classification suggested by Forshaw (1989). Several authors have suggested that three extant genera, Anodorhynchus, Cyanopsitta, and Ara comprise the macaw group (Ridgely 1982, Forshaw 1989, Abramson et al. 1995). These three genera include three, one, and 13 living species respectively (Forshaw 1989).

Several authors have proposed different taxonomic classifications for the macaw group, adding genera or moving species from one genus to another. These taxonomic suggestions are based on external characters such as plumage coloration than in cytogenetic studies, behavioral ecology, or biogeography. Ridgeway (1916) suggested the existence of 12 species of the genus Ara. Low (1990) proposed that the Hahn's or Red-shouldered Macaw, (A. nobilis) should be considered a distinct genus (Diopsittaca nobilis) because it is more morphologically and behavioraly akin to the genus Aratinga than Ara. The genus Rhynchopsitta also is closely related to Ara (Ridgely 1982, Forshaw 1989) and could be considered a small macaw. Sloan (1972) treats the Spix's Macaw (Cyanopsitta spixii) as a species from the genus Ara (A. spixii).

There is scant information about how many kinds of macaws have existed. We only know that all of the six or seven species of macaws endemic to West Indies islands (e.g., Dominican Macaw [Ara atwoodi], Cuban Macaw [A. tricolor]) once occurred in large numbers but are now extinct (Du Tertre 1654, De Rochefort 1658, Sloane 1725, Labat 1742, Browne 1789, Atwood 1791, Clark 1905, Greenway 1958 all in: Snyder et al. 1987). How well differentiated most of these extinct island forms may have been is conjectural because for most of them there are no specimens or bones or even thorough written descriptions. There is some evidence suggesting that most of these West Indian macaws may have diverged from a common ancestor: either the Scarlet Macaw (A. macao) or Green-winged Macaw (A. chloroptera) (Ridgway 1916, Snyder et al. 1987).

## Biochemical Evidence

Although there are many similarities within the three genera and the 17 living species of macaws (Forshaw 1989), there also is a fair amount of variability within this group. When using only external morphometric features to make judgments about evolutionary relationships it is possible to be misled particularly by the process of evolutionary convergence (Smith 1975, Sibley and Ahlquist 1991). Evolutionary convergence is defined as a process by which a similar character evolves independently in two species or group of species (e.g., exposed epidermis on the facial area of the species in the genus *Ara* from the Neotropical region and the Palm Cockatoo (*Probosciger aterrimus*) from the Australian region) (Ridley 1993).

Valentine's (1995) study of derived chromosomes in 13 distinct species of macaws suggested that these species belong to five groups. The main characteristics among these species are changes in chromosome numbers three and eight and the development of a unique chromosome number nine.

The most ancestral chromosome forms are present in the first group which includes the Spix's (*Cyanopsitta spixii*), Blue and Gold (*A. ararauna*), Blue-throated (*A. glaucogularis*), and Severe (*A. severa*) macaws. Within this group the species lack any differences in chromosome morphology and are identical to other parrot genera such as *Aratinga* and *Pionites*. The second group includes the Noble Macaw (*A. nobilis*) which presents a pericentric inversion of chromosome number eight. The third group is only represented by the Yellow-collared Macaw (*A. auricollis*) which has a uniquely derived variation of a band of heterochromatic DNA added into the middle of the long arm of chromosome number three. The fourth group includes the

Scarlet (A. macao), Military (A. militaris), Buffon's (A. ambigua), Green-winged (A. chloroptera), Red-fronted (A. rubrogenys), Hyacinth (Anodorhynchus hyacinthinus), and Lear's (A. leari) macaws, which have developed a unique small acrocentric chromosome number nine. The last group includes only two species, Hyacinth and Lear's Macaws, which, in addition to having the unique chromosome nine, also has developed a inversion of chromosome eight as occurred in the second group.

This evolutionary tree presents the most parsimonious sequence of chromosomal events during macaw evolution. Some of these five separations are also supported by morphometric analysis. The chromosomal data and the morphological information alone are not sufficient to establish the phylogeny of a taxa, including the macaw group. Further field studies on behavioral ecology, embryonic development, and biogeography are needed to establish more suitable phylogenetic relationships in this group.

## The Fossil Record

Sick (1984) suggested that Psittaciformes may have originated in a tropical zone and then radiated to temperate environments such as the Patagonias and United States. The oldest parrot-like fossil known is Archaepsittacus verreauxi from the Tertiary period (Miocene: 25-30 million years BP) and was found near Allier, France (Sick 1984, Forshaw 1989).

Other fossils from the upper Miocene (20 million years ago) have been found in the United States, and still others from the Pleistocene (20,000 year old) have been found in Minas Gerais, Brazil (Sick 1984, Forshaw 1989). Snyder et al. (1987) mentioned that few Psittacine fossils exist in the Caribbean islands and no fossil bones of macaws have been found. This evidence suggests that the parrot group is a very old taxon, but the scarcity of fossils makes it difficult to study its phylogeny.

## Species Description and Morphometrics

The genus *Ara* (Lacepedes, 1799) includes 15 recognized species, and of these, two are now extinct (Forshaw 1989). The most conspicuous characters of the genus are their large body size, moderate to large bill, graduated tails, sexes with the same colormorphic plumage, and exposed epidermis in the facial area (Ridgway 1916, Forshaw 1989).

Adult Scarlet Macaws have feathers of the head, neck, back scapulars, lesser wing coverts, greater part of tail, and under parts, including under wing-coverts with a clear scarlet vermillion color, which is deeper on under parts, and tends to deep poppy red. The middle and proximal greater wing-coverts are orange-yellow (between chrome and deep chrome yellow), some of them, occasionally with a terminal spot of dull greenish or blue green (South America specimens). The distal greater coverts, alula, primary coverts and remiges have an uniform dull cobalt blue and the tertials (i.e., inner secondaries) more tinged with green. The maxilla has mostly a pale brownish yellow color. The mandible, tip of maxilla, and a triangular area on lower basal portion of maxilla, are black. The iris is pale yellow in adult birds and brown on immature birds. The bare skin of the head is pale flesh color or pinkish white. Legs and feet are dusky grayish or blackish (Ridgway 1916, Forshaw 1989).

## Subspecies Taxonomy

The Scarlet Macaw (Linnaeus, 1758 -*Psittacus macao*) has been recognized as a monotypic species (Ridgely 1982, Forshaw 1989). During the last two decades, however, aviculturists have expressed that Scarlet Macaws from Central America and Mexico and South America have some differences in wing plumage color and body size (Smith 1991). Abramson and Thomsen (1995) suggested that there are probably three subspecies of Scarlet Macaws. Their argument, nevertheless, is based on captive bred specimens and they did not provide information on their natural distribution, morphometrics or genetics. Voren (1996) mentioned also that among aviculturists it is common to refer to the Bolivian Scarlet Macaws as the "giant Bolivians." Nevertheless, he suggested that Scarlet Macaws captured in Colombia are smuggled in large quantities into

Bolivia for exporters. The traffic of Scarlet Macaws between countries in Latin America to supply bird dealers and the captive breeding of these different geographical populations make it unacceptable to describe subspecies solely from captive macaws or from doubtful origin.

Captive breeding of Scarlet Macaws in the United States and other countries has been a very common practice for many decades (Hopkinson 1926; Schubot et al. 1992; Abramson 1991, 1996). The captive breeding of Scarlet Macaws from South America with specimens from México or Central America and the encouragement of color mutations (e.g., plumage predominantly white with normal iris, bill, and feet colors) of this species have been common within aviculturists (De Dios and Sweeney 1995, Gabel and Elgas 1995, Voren 1996). Recently, several avicultural organizations (e.g., American Federation of Aviculture) have issued policies to stop hybridizing macaws and other birds (Gabel and Elgas 1995). Aviculturists, particularly in the United States and Philippines, who continue to hybridize macaws and other parrots apparently are driven by curiosity and financial incentives (De Dios and Sweeney 1995). These macaw hybrid offspring usurp the biological value of their parents by diverting genetic material from their respective species.

Recent studies by Wiedenfeld (1994) regarding the morphometrics and color plumage of Scarlet Macaws from known localities suggested that the species should be split in two subspecies, A. macao cyanoptera and A. m. macao. The first possible subspecies historically occurred from México, through Belize, Guatemala, El Salvador, Honduras, to central Nicaragua. The second possible subspecies range from Panama to South America and should be refered as the nominate race (A. m. macao). Specimens occurring in southern Nicaragua and northern Costa Rica should be considered a population in a zone of intergradation between the two races. Further phylogenetic studies on the degree of the genetic divergence and habitat differences on proposed subspecies are needed.

## Geographical Distribution In México

### Historical Distribution

The former range of the Scarlet Macaw in the Neotropics was from north-eastern México to southern Brazil (Ridgway 1916, Forshaw 1989, Ridgely 1981, AOU 1983, Sick 1984, Wiedenfeld 1994). In México, this species was a breeding resident in the states of Tamaulipas, Veracruz, Oaxaca, Tabasco, Chiapas, and Campeche (Friedmann et al. 1950, Ridgway 1916, AOU 1983, Forshaw 1989). In Tamaulipas, this species was found in most of the tropical humid lowlands up to the vicinity of what is today Tampíco City (Salvin and Godman 1879-1904, Sumichrast 1881, Ridgway 1916). In the state of Veracruz it occurred in Túxpan, Uvero, Jesús Carranza, along the riparian forests of the Chalchijapa (Alegro), Solosuchiapa, and Coatzacoalcos Rivers (Salvin and

Godman 1879-1904, Sumichrast 1881, Lowery and Dalquest 1951, Ridgway 1916). In Oaxaca state, there were records in Santa Efigenia, Chimalapa, Tehuantepec City, Cacoprieto, Punta Paloma and Tapanatepec west of Huatulco Port, Niltepec, south of Matias Romero, and Santa Martha or San Miguel Chimalapa (Lawrence 1875, Salvin and Godman 1879-1904, Sumichrast 1881, Ridgway 1916, Binford 1989). In Tabasco, Scarlet Macaws were recorded from the riparian forests along the Macuspana, Chilapilla and San Diego Rivers (Rovirosa 1887 in Brodkorb 1943). In Chiapas, it was found near Tonala, Grijalva River, and in the Selva Lacandona along the riparian forest in the Usumacinta River, Ocotal Lake, and the Jatate (Colorado), Ixcán, Lacantún, Tzendales, San Pedro Salinas, and Lacanja Rivers (Salvin and Godman 1879-1904, Sumichrast 1881, Paynter 1957, Ridgway 1916, Alvarez del Toro 1980, Ridgely 1981, Rangel-Zalazar 1990, González-García 1993, Iñigo-Elias unp. data.). In Campeche, Scarlet Macaws were known in Pacaitún forests along the Candelaria River (Traylor 1941).

## Current Distribution

Currently, there are only two known isolated populations of Scarlet Macaws within México. The largest population is along the riparian tropical forest communities in the Usumacinta drainage basin of the border lands between México and Guatemala. A second remnant population of

Scarlet Macaws exists around the community of San Francisco La Paz, Municipio de Sta. María Chimalapas, Oaxaca along the Río Uxpanapa (M. Lazcano Barrero pers. comm.). The rural community of San Francisco La Paz is protecting a forest remnant called "Cerro Guacamayo" (Macaw Hill) within the Reserva Campesina de los Chimalapas.

## Historical Relevance

### Prehispanic Cultures

Wild birds have been either venerated, trapped, or hunted by Mesoamerican cultures for centuries (e.g., Aztecs, Mayas) to obtain their feathers and meat, or as pets (Sahagún 1577, Valadez and Paredes 1990). Among the Aztecs (1300 - 1500 A.D.), the Scarlet Macaw known as Arara or Xiuhtecutli, was the God of sun and fire. It was also a monarch and the name of the 11th hour (am) of the day (Valadez and Paredes 1990). In Mayan (100 BC - AD 900) mythology the Scarlet Macaw was known as Vucub-Caquix which is interpreted as the sun before its creation (Valadez and Paredes 1990). According to Sahagún (1577) the Aztecs climbed trees to trap macaws and parakeet nestlings to keep them as pets, teaching some of them to speak.

### Macaws and the Pet Trade

Since the 1700s, parrots have continued to be very popular among Mexicans mainly as pets (Salvin and Godman

1888-1904, Ramos 1982, Iñigo-Elias and Ramos 1991). The same is true in many other Latin American and Caribbean countries (Wetmore 1968, Snyder, et al. 1987).

Psittacines have been traded in Mexico for centuries. From 1100 to 1716, ethnic groups, such as Pimas in Arizona, traded green stones for live macaws, particularly Scarlet Macaws, with Mesoamerican cultures (Hargrave 1970). Macaws were kept among these ethnic groups because of their beautiful feathers which were plucked for adornments. So far no artifacts made of macaw bones have been found in the southwestern United States, nor is there any indication of the use of parrots for food. The Scarlet Macaw trade from Mesoamerica to the Pimas in Arizona shows that immature and newly fledged birds (84%, n = 117) were preferred (Hargrave 1970, Thompson 1995). These studies suggest a well organized trade in young macaws originating further to the south, in tropical México.

In the twentieth century, the psittacine trade in Mexico has been documented in several parts of the country. Most of the data available are for exportation (Nilsson and Mack 1980, Nilsson 1981, Ramos 1982) and little information is available on the local trade (Iñigo-Elias 1983, Iñigo-Elias and Ramos 1991). Currently, a few Mexican universities are conducting studies on the impact of this trade on wild parrot populations in the country. Among these centers are Universidad Michoacana and the Instituto Tecnológico y de Estudios Superiores de Monterrey (ITESM).

Between 1970 and 1982, Mexico was a major exporter of live birds for the pet trade from the Neotropics, exporting an average of 14,500 psittacines annually to the United States (Iñigo 1986, Iñigo-Elias and Ramos 1991). In 1979, Mexico was the most important Latin American supplier of wild birds to the United States (Nilsson 1981).

In 1982, the General Wildlife Directorate, division of the Ministry of Agriculture and Hydraulic Resources (SARH) introduced a ban on "Control Bases and Regulations of Exportation and Importation of Wildlife and Derived Products." This order prohibited all commercial export and import of live wildlife and wildlife products native to the country (SFF 1982, Rodriguez 1986). This ban has reduced the legal exportation (i.e, scientific or for zoos) trade of parrots from Mexico.

Table 2-1. Morphometrics of the Scarlet Macaw. Measurements are range and arithmetic mean in mm. Measurements are following Baldwin _et_ _al_. (1931) descriptions.

| Body parts | Male |  | Female |  |
|---|---|---|---|---|
|  | Range mm | Mean mm | Range mm | Mean mm |
| Body length | 742-920 | 841 | 795-950 | 848 |
| Wing chord | 355-426 | 401 | 368-410 | 391 |
| Tail length | 387-649 | 528 | 480-610 | 529 |
| Tarsus length | 33-38 | 36 | 33-36 | 35 |
| Culmen length | 62-73 | 69 | 59-70 | 67 |

Samples: male _n_ = 18, female _n_ = 13
* measurements source: Ridgway 1916 and Forshaw 1989.

# CHAPTER 3

# COMPARISON OF SCARLET MACAW SAMPLING DETECTABILITY BY WALKING AND RIVER TRANSECT SURVEYS IN CONTINUOUS AND DISTURBED FORESTS IN THE USUMACINTA DRAINAGE BASIN OF MEXICO AND GUATEMALA

## Introduction

Scarlet Macaws (*Ara macao*) are among the most endangered avian species in México and northern Central America (Ridgely 1982, Forshaw 1989, Howell and Webb 1995). This is an important economic species, pressured heavily by villagers, pet dealers, aviculturists, zoos, and by ecoturism agencies. At the same time, biologists and conservationists have used macaws as "umbrella" species (i.e., species that require large areas to maintain viable populations and by which conservation of their habitat may protect the habitat and populations of many other restricted or less wide ranging species) to structure plans to conserve the tropical rainforest ecosystem in Central and South America.

The governments of México, Guatemala, Belize, and Honduras have taken some actions to protect macaws. These include listing these species as threatened in national and international laws and establishing protected areas within their habitats. Nevertheless, these measures are insufficient for the conservation of macaws and their habitats. The Scarlet Macaw population is under such pressure in Mexico and Guatemala that it could be extirpated "completely from [the] region within a few years" (Howell and Webb 1995) if ecologically sound programs and extensive management projects are not implemented and local communities are not involved in the conservation efforts.

Therefore, it is important to develop and explore alternative conservation management measures rather than merely setting aside protected areas and listing species as "threatened". Adequate conservation measures require detailed knowledge of the species' population biology and ecology.

This study attempts to document the spatial and temporal distribution of Scarlet Macaws using two censusing techniques in continuous and disturbed forests. The purpose of this study is to report an intensive and extensive technique for counting Scarlet Macaws in a tropical humid forest, in the Usumacinta drainage basin, on the border of México and Guatemala.

The main objectives of this study are: (1) to determine the relationship between vegetation structure (canopy cover, vegetation obstruction to horizontal vision) and macaw detectability in tropical forests; and (2) to identify, test, and estimate the limitations of standard survey methods used to count birds in continuous and disturbed forest by using two main methods: walking transects and river transects by boat, and to suggest alternatives to cope with potential survey problems.

## Study Sites

This part of my study was conducted only in Mexican territory from July 1989 to August 1990 at two sites: a continuous forest encompassing both Montes Azules and Lacantún Biosphere Reserves (hereafter MABR-LBR), and in a disturbed landscape with diverse forest remnants surrounded by different agroecosystems (e.g., cacao plantations) in the Marques de Comillas Region (hereafter MCR), in the southern portion of the Selva Lacandona region of Municipio of Ocosingo, state of Chiapas, México. The northern portion of MCR borders with the Departments of Huhuetenango and Quiche, Guatemala (Figure 3-1).

The Selva Lacandona is very heterogenous in topography, climate, soils, and vegetation. The region is crossed by a system of parallel mountains, ranging from 500 to 2,000 m and running primarily from northwest to southeast in Méxican territory and from southwest to northeast in the Sierra of Cuchumatanes, Guatemala (CILA 1987 a, de Vos 1988). These mountain systems are divided by ten narrow, long river valleys in México and two in Guatemala, that gradually form the drainage of the Usumacinta River (CILA 1987b, Fig. 3-1). The climate is characterized by three main regimes: (1) hot-humid with summer rainfall and scattered winter rains with the driest month having less than 60 mm of precipitation (Köppen classification modified by García 1973); (2) Semi-hot with a mean annual temperature lower than 22°C and the coldest month of the year with a grater temperature of 18°C (Köppen classification modified by García 1973); and (3) hot-humid with rainfall all year long, the driest month having more than 60 mm of precipitation (Köppen classification modified by García 1973) (CETENAL 1974; CILAc 1987; Meave del Castillo 1983, 1990). In general there are two rainfall peaks during the year, one from June to July and one from September to October; the mean annual rainfall is ≈ 2,500 mm (range 1,000-5,000 mm); the mean temperature is ≈ 24°C (range 20-27°C) (CILA 1987c,d,e,f; CILA unpublished data 1989-1990). The area is mostly limestone with some sandstone and volcanic extrusions. Several soil types dominate the region: litosols, fluvisols, andosols, luvisols, acrisols, cambisols, gleysols, and rendzinas (CILA 1987g,h,i,j; Casco 1990; Garcia-Gil and Hupb 1992).

The vegetation of the Selva Lacandona occurs within the physiographic region known as the Eastern Highlands (Mulleried 1957; CILA a, j) that extends southward into Guatemala. This region supports five main natural vegetation types: (1) dominant vegetation is lower montane rain forest with patches of (2) short-tree savanna and (3) palm forest. Evergreen and (4) semi-evergreen seasonal forest are common in the northern portion of the area and (5) montane rain forest is present only on the crests of the highest ridges. Tropical forest is present in flat areas surrounding the upper drainage of the Usumacinta River (Miranda 1952, 1961; Pennington and Sarukhan 1968; Breedlove 1973; Meave del Castillo 1983, 1990; Rzedowski 1983).

My research was conducted in part of the Usumacinta drainage basin that includes the rivers Jatate, Ixcán, Puerto Rico, Lacantún, Chájulillo, Miranda, Lagartos, Manzanares, Tzendales, San Pedro, El Bravo, Lacanja, Aguilar, and the Usumacinta (Table 3-1). Most of this research was conducted in two study sites, MABR-LBR and MCR, which are separated by the Jataté and Lacantún Rivers in the southern region of the Selva Lacandona (16°,00′ - 16°,55′ latitude N and 90°,35′ - 91°,10" longitude W). The two study sites were adjacent to each other on opposite banks of the river. In MABR-LBR more than 400,000 ha of tropical forest is still unfragmented. Here the understory is dominated by spineless palms (Chamaedora sp.) in dry soils (Meave del Castillo 1983, 1990) and by spiny palms (Bactris sp.) in swampy soils (Iñigo-Elias pers. obs.). This forest has a fairly even closed canopy averaging 35 m in height with some emergent trees up to 65 m in height. The elevation in the area ranges from 80 to 1,000 m. The MCR, with approximately 160,000 ha the forest, has been largely deforested and fragmented (O'Brien 1995, Arizpe et al.

1996), particularly at the edges of the Lacantún River and Salinas River, for agriculture and cattle ranching. The original vegetation types were very similar in both MCR and MABR-LBR (Iñigo-Elias pers. obs.). In this region 46 rural villages (i.e., ejidos) exist with a combined population of more than 10,000 people (Mauricio-Leguízamo et al. 1984). The elevation here ranges from 80 to 150 m.

## Materials and Methods

I collected data on the abundance of Scarlet Macaws in both areas, MABR-LBR and MCR using two survey methods: walking and boat transect censuses. On the walking surveys I gathered and analyzed data on: (1) detection modes (numbers seen vs heard); (2) morning and afternoon; (3) forest strata; (4) calls versus rainfall, and; (5) frequencies of perching or flying solitary macaws and flocks. On the boat transect surveys I collected data on (1) morning and afternoon, (2) forest strata, and (3) frequencies of perching or flying solitary macaws and flocks. I was not able to use calls versus rainfall due to the noise of the boat.

### Walking Transect Surveys

In order to minimize pseudoreplication (Hulbert 1984, James and McCulloch 1985, Kamil 1988, Eberhardt and Thomas 1991, I carefully established 12 walking line transects at each site (spatial survey transects) and surveyed each of them in 12 continuous months (temporal survey transects). To reduce bias associated with time of day, during each month at both sites (MABR-LBR and MCR) I conducted six transects during am h and six in pm h. These were perpendicular to a 120 km stretch of the Lacantún River (Figure 3-1). The first two months of field work (July to August 1989) were dedicated to establishing the transects and testing the field equipment and survey methods. Each of these transects was 1,100 m in length; they started at the edge of the Jataté and Lacantún Rivers and were oriented at a 90° angle into the forest to progressively move away from the river edge (Morrison _et_ _al_. 1992). I counted birds within a range of 0-200 m on either side of the center of the transect.

Transect lines in the continuous forest (MABR-LBR) and in the disturbed forest (MCR) were chosen systematically. The initial transect location was selected at the base of "El Cañon de Colorado" (Jataté River), near to the southwest boundary of MABR (Fig. 3-1). Each successive transect, at each site of the Lacantún River, was located between 10 and 15 km along the river (down current) from the previous transect to minimize double counting of birds.

I conducted a systematic surveying effort using a team of the same three observers. Each transect was surveyed once per month, starting in September 1989 and ending in

August 1990. I started with transect I-MABR-LBR and I-MCR and ended with XII-MABR-LBR and XII-MCR. During each monthly survey two transects were surveyed each day, one in MABR-LBR and another in MCR. To minimize bias associated with time of day, I alternated the order on which I conducted the survey at each site. For example, if during the same day a transect in MABR was conducted in the morning (0700-1030 h) and another transect in the MCR traversed in the afternoon (1200-1530 h) the reverse order was followed the next day.

In order to increase the probability of detecting more individuals along my transects, I modified and combined two counting techniques: (1) a modified standard line transect (Emlen 1971; Burnham et al. 1980; Ralph and Scott 1981, SCNP 1981, Verner 1985, Seber 1986, Buckland and Turnock 1992, Bibby et al. 1992, Ornelas et al. 1993), combined with (2) line transect stations (Burnham et al. 1980, Bibby et al. 1992). I placed 5 fixed stations at 250 m intervals along each transect, starting 100 m from the edge of the river (e.g. 0, 250, 500, 750, 1,000 m).

I followed the line transect technique suggestions for the analysis and inference procedures for mobile populations (Burnham et al. 1980). The line transect technique assumes that: (1) all birds located on the transect line are always detected; (2) that birds do not move before being seen or flushed; (3) sighting distances $r_i$ and sighting angles $\theta_i$ are measured exactly; (4) sightings are independent events (Burnham et al. 1980). These assumptions can be violated in different ways when conducting field line transects, particularly with very mobile populations in thick tropical forests (Wagner 1981, Bart 1985, Drumer and McDonald 1987, Waide and Narins 1988, Quang 1991, Turnock and Quinn 1991, Bibby et al. 1992). These assumptions were considered when obtaining field data so as to minimize such violations and their potential effects on my analysis.

The survey technique involved an observer (always myself) moving quietly along each transect and stopping within stations. Birds were detected visually or aurally between and within stations on either side of the transect. For each sighting I recorded the bird's estimated sighting distance ($r_i$) or observer-object distance and sighting angle ($\theta_i$) with respect to the transect to reduce possible double counting birds and to analyze the data for line transect densities (Burnham et al. 1980).

For each individual or flock detected I recorded the following variables: 1) number of individuals; 2) day; 3) time of the day (h and min); 4) direction of flight (N, S, E, W, NE, SE, NW, SW), 5) transect number; 6) position of the observer (O) along the transect; 7) sighting angle ($\theta_i$) from the observer to the bird; 8) sighting distance ($r_i$) from the observer to the bird; 9) visual or aural detection; 10) behavior (e.g., perching, flying, calling); 11) if perching type and height of perch and height of the bird in the perch; 12) habitat strata (understory <30 m height, canopy ≥30-50 m height, upper canopy ≥50-≥100 m, and sky > 100 m height); and 13) habitat category (riparian forest, forest interior, pasture, annual crop, perennial plantations).

Macaw detectability was correlated with vegetation obstruction within and between transects and between sites (continuous, disturbed). Thus I placed one plot (11.5 m radius) at 100 m intervals along each transect, starting at the edge of the river (0 m) and continuing into the forest until 1,100 m. I also established plots at the stations in 250 and 750 m bringing the number of plots per transect to 14. At each plot I recorded information on: (1) the percentage of overstory canopy cover using an spherical convex densiometer (Lemmon 1956, Cook et al. 1995); and (2) the percentage on the degree of obstruction to horizontal vision, using a fixed board 1.5 X 1.5 m (Gysel and Lyon 1980).

### River Transect Surveys

In the river transects I followed the same procedures described above for the walking transect surveys. The main difference in the sampling design was that I used 11 transects along the Jataté and Lacantún Rivers (Fig. 3-1). Each transect ran from upstream to downstream. I conducted a systematic surveying effort using a small boat with a outboard motor (40 hp). Each transect was surveyed once per month, starting in September 1989 and ending in August 1990. I started with transect I-river and ended with XI-river. During each monthly survey one transect was surveyed each day, looking at both sides of the boat; left (MABR-LBR) and right (MCR). To minimize bias associated with time of day, I alternated the order in which I conducted the survey at each transect. For example, during the first month I conducted transect I in the morning (0600-0700), the next day I surveyed transect II in the afternoon (1700-1800) and so on. The following month transect I was surveyed in the afternoon, II in the morning, and so on.

## Data Analysis

### Modes of detection

I calculated and plotted the detections of macaws per 13 km by pooling counts, maximum population size (i.e., the month with the most macaws detected of the 12 monthly surveys at each transect), per month (n=12 transects) of individuals recorded in each of the two detection categories (seen or heard) for each site (MABR-LBR and MCR). In order to determine whether the two sites (MABR-LBR and MCR) differed in the proportion with which they fall into the two categories (seen or heard) I performed a $G_{adj}$ test of independence (Sokal and Rohlf 1981) with an $\alpha = 0.05$. $H_0$:

Continuous (MABR-LBR) and disturbed (MCR) habitat Scarlet Macaws show equal proportions in their detection category (seen or heard). To ascertain whether the two sites (MABR-LBR and MCR) differed in the monthly proportion which they occurred the two categories (seen or heard) I performed a Mann-Whitney U-test for two samples (Sokal and Rohlf 1981) with an $\alpha = 0.05$. $H_0$: Seen (or heard) macaws in the continuous (MABR-LBR) and disturbed (MCR) forest show equal proportions of detection.

### Daily abundance

I calculated and plotted the percentage of the maximum number of macaws recorded from one of the 12 monthly surveys (i.e., maximum population size of macaws) either during the morning 0700-1030 or afternoon 1200-1530 categories and for each site (MABR-LBR and MCR) and for each of the survey methods (walking and river transects). To determine whether the two sites (MABR-LBR and MCR) differed in the proportion of the population which occurred in the two categories (AM or PM) I performed a $G_{adj}$ test of independence (Sokal and Rohlf 1981) $H_0$: Scarlet Macaws in the continuous (MABR-LBR) versus disturbed (MCR) forests showed equal proportions in the time category (AM or PM).

### Detection forest-strata

I calculated and plotted the maximum population size of individuals recorded, in percentage, for each of the three forest-strata categories (understory, <30 m; canopy ≥30-<50 m; and upper canopy ≥50 ≥100 m) from the total number of records for each site (MABR-LBR and MCR). To determine whether the two sites (MABR-LBR and MCR) differed in the proportion with which they fell into the four categories (understory, canopy, upper canopy, sky) I performed a G-test of independence probability (Sokal and Rohlf 1981) with an $\alpha = 0.05$. $H_0$: Scarlet Macaws found in continuous (MABR-LBR) and disturbed (MCR) habitats show equal proportions in the habitat strata categories (understory, canopy, and upper canopy-sky). Data from upper canopy and sky categories were pooled because of their small sample sizes.

### Solitary and group frequencies

I calculated the total number of macaws detected as solitary individuals, pairs, trios, or groups (≥ 4 birds) either flying or perching at each of the sites (continuous and disturbed forests). I estimated this for both walking and river transect surveys. To determine whether the two sites (MABR-LBR and MCR) differed in the proportion with which macaws fell into the four categories (solitary, pairs, trios, groups) I performed a G-test of independence (Sokal and Rohlf 1981) with an $\alpha = 0.05$. $H_0$: The frequency of solitary, pairs, trios and groups of Scarlet Macaws do not differ between continuous (MABR-LBR) and disturbed (MCR) habitats.

### Dry-rainy abundance

I calculated and plotted the maximum population size of individuals recorded during the rainy (June, July, August, September, and October) and dry (November, December, January, February, March, April, and May) seasons from the total number of records for each site (MABR-LBR and MCR). To determine whether the two sites (MABR-LBR and MCR) differed in the proportion with which they occurred in the two categories (rainy or dry) I performed a Pearson (Homogeneity) $X^2$ test (Sokal and Rohlf 1981) and a Fisher exact probability test (Siegel 1956) with an $\alpha = 0.05$. $H_0$: Scarlet Macaws in continuous (MABR-LBR) and disturbed (MCR) habitats showed equal proportions in the rainy-dry category. All statistical analyses were performed using the SYSTAT program (Wilkinson 1990).

## Results

A total of 12 walking transect surveys were conducted, excepting five transects, three in the Montes Azules and Lacantún Biosphere Reserves (MABR-LBR) and two in the Marques de Comillas Region (MCR) (see Table 3-1) that were omitted due to heavy rains from Hurricane Hugo which flooded the forest. During the 12 survey months, I conducted a total of 141 transects at both sites (Table 3-1) covering an area of 5.28 $Km^2$ in both sites. Approximately equal survey effort (time) was spent in MABR-LBR (382 h) and MCR (376 h)

($\underline{Z}_{0.05[12,12]} = -1.156$, $\underline{P} = 0.248$, table 3-1). There was little variation among transects with respect to mean and range of canopy cover in MABR-LBR ($\underline{t} = 6.17$, $\underline{P} = <0.0001$, Table 3-1); mean canopy cover was more heterogeneous ($\underline{F} = 14.58$, $\underline{P} = <0.0001$) and much lower in the MCR (Table 3-1).

There was great variation on the percent of vegetation obstruction to the horizontal vision (%VOHV) between continuous and disturbed transects ($U_{0.05[240, 240]} = 12565$, $P = < 0.0001$; Table 3-1). There was more homogeneity among transects with respect to the mean and range of the %VOHV (MABR-LBR $\underline{F} = 18.22$, $\underline{P} = 0.076$, df = 11; MCR $\underline{F} = 14.810$, $\underline{P} = 0.191$, df = 11).

With the walking transects in the continuous forest (MABR-LBR) the density of Scarlet Macaws was 3.86 macaws/$Km^2$ and in the disturbed forest (MCR) the density was 5.80 macaws/$Km^2$. A Mann-Whitney U Test showed no significant difference between continuous (MABR-LBR) and disturbed forest (MCR) populations ($U = 0.235$, $\underline{P} = 0.813$). No estimates were possible with the data from river transects because the high number of zeros.

## Method of Detection

Of the total number of individual macaws recorded in MABR-LBR (n = 229) approximately 11.3% were audible records, 88.6% were visual. In MCR, (n = 349) approximately 4.29% were audible records, 95.71% were visual. In both MABR-LBR and in MCR, macaws were significantly more often detected by sight than by sound ($G_{adj}$ Test of Independence = 10.82, df 1, $\underline{P}$ >0.001; Figure 3-2). Aural detections peaked slightly in September, March, and July in both continuous and disturbed forests, whereas visual detections remained high between September and December, before the peak of the nesting activity in the Usumacinta drainage basin area (January-June) (Fig. 3-2). More macaws were detected in the disturbed landscape (MCR) than in the continuous forest (MABR-LBR).

### Daily Abundance

Of the total Scarlet Macaws recorded in walking transects in MABR-LBR (n = 229) approximately 67.7% were recorded in the morning surveys and 32.3% during the afternoon surveys (Figure 3-3a). Similar distribution pattern occurred in MCR (n = 325) approximately 68.6% were recorded in the morning surveys and 31.4% during the afternoon surveys. A $G_{adj}$ test of independence for the walking transect data showed no significant difference in the proportion detected in morning versus afternoon for both continuous and disturbed sites ($G_{adj}$ = 0.0533, 0.5 < $\underline{P}$ < 0.9, df = 1; Fig. 3-3a).

Of the total macaws recorded in river transects in MABR-LBR (n = 90) approximately 42.3% were recorded in the morning surveys and 57.7% during the afternoon surveys

(Figure 3-3b). A similar distribution pattern occurred in MCR (n = 114) approximately 39.5% were recorded in the morning surveys and 60.5% during the afternoon surveys. A $G_{adj}$ test of independence for the river transect data showed no significant difference in the proportion detected in morning versus afternoon for both continuous and disturbed sites ($G_{adj} = 0.1561$, $0.1 < \underline{P} < 0.5$, df = 1; Fig. 3-3b).

## Detection and Forest-Strata

Macaws were detected more in the canopy (30 m to 50 m) forest at both MABR-LBR and MCR than in any other habitat strata categories (Fig. 3-4). The detection of macaws in the canopy was almost the same for walking and river transects. A $G_{adj}$ test of independence showed that macaws found in MABR-LBR and MCR had a significant difference in the proportion with which they were detected in the three forest strata categories (MABR-LBR, $G_{adj} = 41.80$, $\underline{P} = < 0.0001$, df 2; MCR, $G_{adj} = 37.29$, $\underline{P} = 0.0001$, df 2).

## Solitary and Group Frequencies

Macaws, were detected more often in flight as pairs than any of the other three association categories (solitary, trios, and groups = ≥ 4 individuals) in both MABR-LBR and MCR walking transects (Table 3-3). A $G_{adj}$ test of independence shows that macaws found in MABR-LBR and MCR (by walking transects) differed significantly in the proportion with which they were detected in either of the association categories ($G_{adj}$ = 18.75, 0.001 < $\underline{P}$ < 0.005, df 6). In general, the same proportion of pairs were detected in the continuous and the disturbed forest (Table 3-3).

## Dry-Rainy Season Abundance

Figure 3-5 shows temperatures (°C) and precipitation (mm) in the study area during the study period. Figure 3-6 shows the relationship of the maximum population size of macaws (i.e., maximum number of macaws detected per month [12] per transect [12]) in relation to mean monthly precipitation (mm). A Spearman correlation coefficient indicated no relationship between macaw abundance and rainfall (MABR-LBR $\underline{r}_s$ = 0.141, $\underline{P}$ = > 0.05, n = 12; MCR $\underline{r}_s$ = -0.305, $\underline{P}$ = > 0.05, N=12).

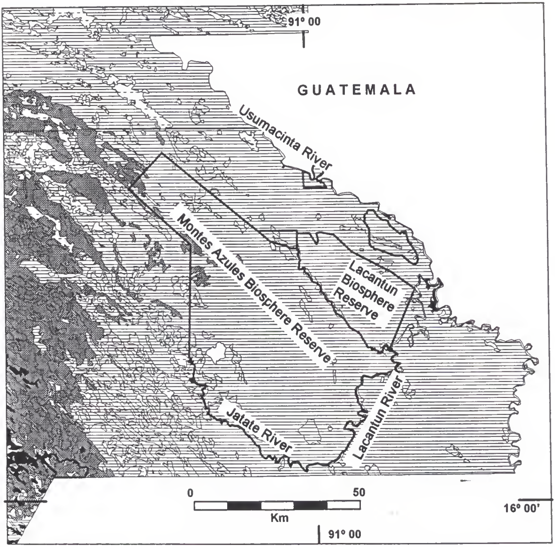

Figure 3-1. Study site and major landscapes in the Usumacinta drainage basin of México and Guatemala during 1989-1990.

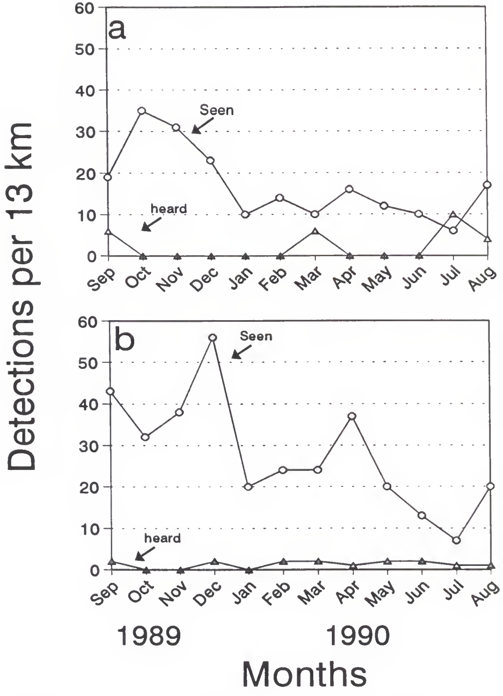

Figure 3-2. Scarlet Macaws heard calling and seen by month during walking and river transects in both continuous and disturbed forests in the Selva Lacandona, region México and Guatemala during August-December 1989 and January-August 1990. a) Macaws seen and heard in continuous forest; b) Macaws seen and heard in disturbed forest.

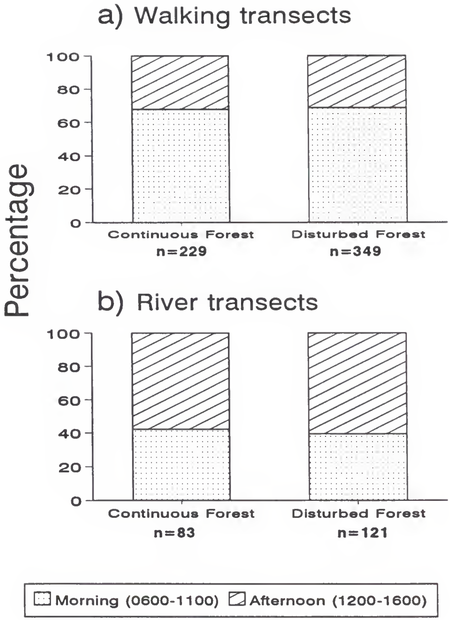

Figure 3-3. Percentage of Scarlet Macaws detected during morning (0600-1000) and afternoon (1200-1500) surveys in the Selva Lacandona, region of Chiapas, México during August-December 1989 and January-August 1990. a) Walking transects in the continuous and the disturbed forests; and b) River transects in the continuous and the disturbed forests.

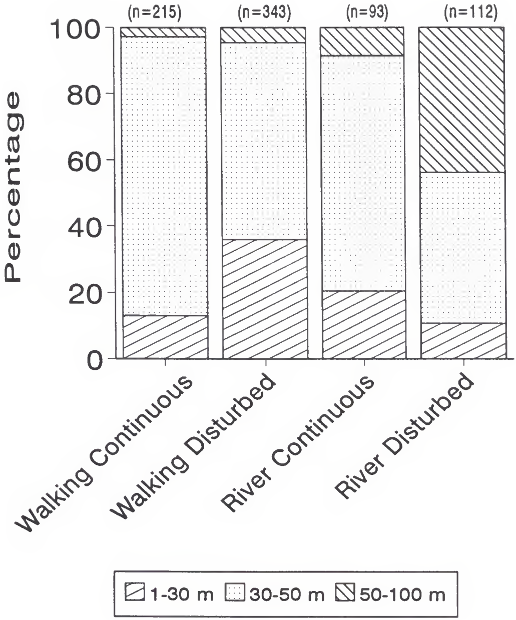

Figure 3-4. Percentage of individuals observed in each of the four habitat strata: understory (1-30 m), canopy (30-50 m), upper canopy (50-100 m) and sky (> 100 m) in both the continuous versus the disturbed forests in the Selva Lacandona, region of Chiapas, México during August-December 1989 and January-August 1990.

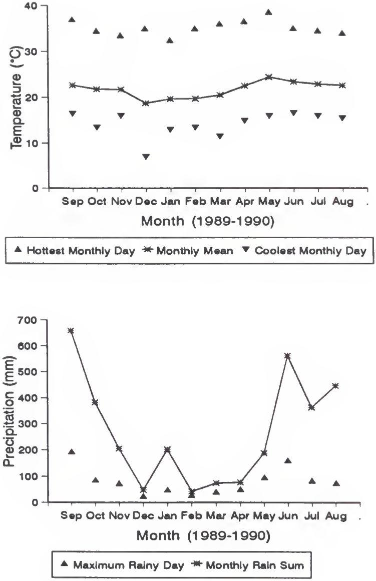

Figure 3-5. Temperature (°C) and precipitation (mm) data in the Usumacinta drainage basin of México and Guatemala during August-December 1989 and January-August 1990. Data represents the mean monthly temperature and maximum monthly precipitation average from five meteorological stations (CILA unp. data, CFE unp. data) in the study area.

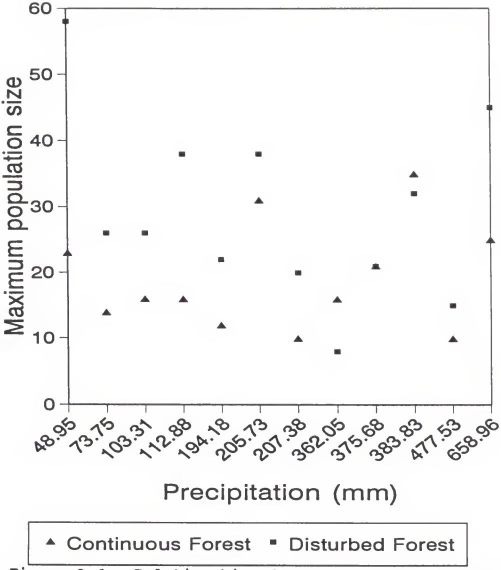

Figure 3-6. Relationship of Scarlet Macaws detected calling to rainfall in the Usumacinta drainage basin of México and Guatemala during August-December 1989 and January-August 1990. a) Continuous forest; and b) Disturbed forest.

Table 3-1. Description of 24 1.1-km walking line transects in continuous tropical forest and disturbed landscapes in the Usumacinta drainage basin of México, 1989-1990.

| Transects | No of surveys | Effort (h)$^1$ | Elevation range (m)$^2$ | % Canopy cover |  |  | % V. O. H. V. |  |
|---|---|---|---|---|---|---|---|---|
|  |  |  |  | Mean$^3$ | Range | SE | Mean$^4$ | SE |
| Continuous forest transects (Montes Azules and Lacantún Biosphere Reserves) |  |  |  |  |  |  |  |  |
| I | 11 | 32.3 | 324-125 | 87.7 | 95-81 | 1.02 | 30.40 | 4.56 |
| II | 11 | 29.1 | 146-107 | 86.8 | 92-77 | 1.23 | 53.09 | 7.77 |
| III | 12 | 33.1 | 128-120 | 89.1 | 92-82 | 0.71 | 49.63 | 5.17 |
| IV | 12 | 34.2 | 116-102 | 85.1 | 92-80 | 0.90 | 68.08 | 2.55 |
| V | 12 | 32.4 | 123-112 | 85.8 | 92-70 | 1.38 | 70.01 | 4.84 |
| VI | 12 | 32.1 | 116-96 | 84.1 | 89-77 | 1.00 | 63.47 | 2.35 |
| VII | 12 | 32.3 | 104-93 | 84.7 | 91-62 | 1.88 | 65.01 | 3.18 |
| VIII | 12 | 31.2 | 110-97 | 88.2 | 94-79 | 0.92 | 40.01 | 7.48 |
| IX | 12 | 32.1 | 104-95 | 81.8 | 89-51 | 2.60 | 57.70 | 14.48 |
| X | 12 | 32.6 | 104-91 | 87.5 | 91-83 | 0.73 | 60.78 | 4.96 |
| XI | 12 | 32.1 | 115-100 | 86.5 | 96-82 | 0.99 | 67.70 | 5.78 |
| XII | 11 | 28.1 | 100-95 | 85.7 | 88-79 | 0.72 | 66.93 | 2.81 |
| Total | 141 | 381.6 |  |  |  |  |  |  |
| Disturbed forest transects (Marques de Comillas Region) |  |  |  |  |  |  |  |  |
| I | 11 | 29.2 | 134-119 | 22.3 | 77-0.1 | 7.14 | 14.64 | 8.96 |
| II | 11 | 32.1 | 130-106 | 80.3 | 91-11 | 5.55 | 38.48 | 9.89 |
| III | 12 | 32.5 | 164-94 | 80.8 | 92-45 | 4.34 | 45.40 | 11.70 |
| IV | 12 | 32.1 | 107-94 | 56.3 | 89-0.1 | 9.30 | 19.63 | 12.31 |
| V | 12 | 29.3 | 138-100 | 23.2 | 74-0.3 | 8.75 | 25.40 | 11.63 |
| VI | 12 | 31.4 | 100-96 | 73.8 | 86-27 | 3.89 | 66.16 | 4.10 |
| VII | 12 | 31.5 | 112-98 | 32.2 | 86-0.1 | 9.63 | 14.64 | 11.93 |

| Transects | No of surveys | Effort (h)[1] | Elevation range (m)[2] | % Canopy cover Mean[3] | % Canopy cover Range | % Canopy cover SE | % V. O. H. V. Mean[4] | % V. O. H. V. SE |
|---|---|---|---|---|---|---|---|---|
| Continuous forest transects (Montes Azules and Lacantún Biosphere Reserves) | | | | | | | | |
| VIII | 12 | 33.1 | 118-112 | 40.8 | 85-0.1 | 9.41 | 31.55 | 19.64 |
| IX | 12 | 32.1 | 100-92 | 20.2 | 70-0.1 | 6.61 | 0 | - |
| X | 12 | 33.2 | 104-92 | 49.6 | 86.0.1 | 10.6 | 30.79 | 18.83 |
| XI | 12 | 31.3 | 102-92 | 54.1 | 98-0.1 | 9.62 | 28.48 | 13.40 |
| XII | 12 | 28.3 | 100-98 | 27.2 | 79-0.1 | 9.15 | 0 | - |
| Total | 142 | 376.1 | | | | | | |

[1] Total hours and minutes spent surveying at each transect during 12 continuous months.

[2] Maximum and minimum altitude measurements obtained from the mean of 6 readings in five stations from the river edge into the forest or landscape (0, 350, 600, 850, 110 m) at each transect with a Thommen TX-12 Altimeter/Barometer.

[3] Obtained from 56 spherical densiometer readings along each transect, every 100 m from 0 m (river edge) to 1100 m and at points 350 m and 850 m.

[4] Percentage of vegetation obstruction to horizontal vision (%VOHV), obtained from two readings (left and right) from 14 points along each transect, from 0 m (river edge) to every 100 m until 1100 m and at points 350 m and 850 m.

Table 3-2. Description of 11 10.5-km river transects in the Usumacinta drainage basin of México and Guatemala during 1989-1990.

| Transects | No of surveys | Effort (h)[1] | Elevation Mean (m)[2] |
|---|---|---|---|
| I | 11 | 32.3 | 125 |
| II | 11 | 29.1 | 121 |
| III | 12 | 33.1 | 120 |
| IV | 12 | 34.2 | 116 |
| V | 12 | 32.4 | 112 |
| VI | 12 | 32.1 | 96 |
| VII | 12 | 32.3 | 95 |
| VIII | 12 | 31.2 | 95 |
| IX | 12 | 32.1 | 95 |
| X | 12 | 32.6 | 95 |
| XI | 12 | 32.1 | 95 |
| Total | 141 | 381.6 | |

[1] Total hours and minutes spent surveying at each transect during 12 continuous months.

[2] Mean altitude in meters above sea level obtained from six readings at the edge of the rivers in the initial point of each river transects with a Thommen TX-12 Altimeter/Barometer.

Table 3-3. Number and percentage (%) of flying or perching Scarlet Macaws during 283 three observer walking transect samples in the continuous and the disturbed forests in the Usumacinta drainage basin of México and Guatemala during August-December 1989, and January-August 1990.

| | Flying | | | | | | | | Perching | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Solitary | | Pairs | | Trios | | Groups | | Solitary | | Pairs | | Trios | | Groups | |
| | N | % | N | % | N | % | N | % | N | % | N | % | N | % | N | % |
| Continuous | | | | | | | | | | | | | | | | |
| Walking | 4 | 2.0 | 144 | 72.3 | 15 | 7.5 | 36 | 18.1 | 0 | 0 | 16 | 32 | 9 | 18 | 25 | 50 |
| River | 0 | 0 | 18 | 29.5 | 9 | 14.7 | 34 | 55.7 | 0 | 0 | 14 | 41.2 | 12 | 35.3 | 8 | 23 |
| Disturbed | | | | | | | | | | | | | | | | |
| Walking | 19 | 6.8 | 168 | 56.4 | 18 | 1.7 | 93 | 31.2 | 5 | 7.3 | 36 | 52.9 | 6 | 8.8 | 21 | 31 |
| River | 1 | 1.4 | 18 | 26.5 | 15 | 22 | 34 | 50 | 0 | 0 | 2 | 5 | 0 | 0 | 42 | 95 |

# CHAPTER 4
# NESTING SITES, NESTING HABITAT, AND NESTING CAVITY AVAILABILITY OF SCARLET MACAWS IN THE USUMACINTA DRAINAGE BASIN OF MEXICO AND GUATEMALA

## Introduction

Little is known about the biology and ecology of macaws in the wild. They are obligate cavity-nesters, highly gregarious, and occur primarily in riparian tropical evergreen forests from México to Brazil (Forshaw 1989, Munn 1994, Abramson et al. 1995). Until recently, few studies have been conducted to understand the natural breeding biology of Ara species (Marineros 1993, Munn 1994, 1995; Bjork and Powell 1995; Nyncander et al. 1995).

Availability of possible nesting sites can limit the number of individuals that breed. Availability of suitable nesting cavities and potential sites for cavities (i.e., snags, dead limbs) may also limit breeding populations of secondary cavity nesters (i.e., nonexcavators) (Sedgwick and Knopf 1990, Li and Martin 1991, Newton 1994), including psittacines (Saunders 1979, Snyder et al. 1987). Data on the nesting ecology, nesting site characteristics, and cavity availability is very limited in psittacines (Snyder et al. 1987, Saunders 1979, Emison et al. 1994, Enkerlin-Hoeflich 1994; Nyncander et al. 1995).

To what extent natural cavities are limiting in the Usumacinta study region and how this may affect the breeding population is an important issue for conservation and management of the endangered Scarlet Macaw, in Mexico and north Central America. These questions may be addressed by studying the availability and distribution of natural cavities in the region as well as by documenting the characteristics of nesting hollows. The nesting ecology of this macaw provides insight into the species' reproductive potential and this information is needed to design conservation strategies to enhance the chances for its survival in México and northern Central America. In this study I climbed nesting trees and potential cavities and collected information on the characteristics and availability of cavities used by macaws to breed in the study area.

## Study Area and Methods

From 1989 through 1990 and 1993 I studied Scarlet Macaw nesting ecology and biology in the Usumacinta drainage basin of México and Guatemala. Data on nesting site ecology, nesting cavity characteristics, and availability of suitable nest hollows were collected intensively in 1993. I studied the breeding biology of Scarlet Macaws in a 52,000 ha study area at 138 m in the riparian forests and agroecosystems along the Mexico-Guatemala border (including the Jataté, Ixcán, Chajulillo, Miranda, Lacantún, Lacanja, Aguilar, and Usumacinta rivers) (See Fig. 3-1 in Chapter 3). The study area consisted of two main vegetation and land use types, a continuous forest, and a disturbed landscape divided by the Jataté, Lacantún and Usumacinta rivers. The first area included the Montes Azules Biosphere Reserve, the Lacantún Biosphere Reserve, and the Yaxchilán Natural Park in México and the Sierra del Lacandón National Park and the buffer area of the Maya Biosphere Reserve in the Department of Petén in Guatemala (hereafter MABR-LBR-YNP-SLNP-MBR). This is a continuous tropical evergreen forest with dominant species such as Schizolobium parahybum, Licania platypus, Ficus sp., Terminalia amazonica, Ceiba pentandra, Swietenia macrophylla, Stemmadenia donnell-smithii, with patches of entangled riparian associations of bamboo (Guadua aculeata), giant grass (Arundo donax), understory spiny palms (Bactris trichophyla) and isolated emergent palms such as Corozo (Scheelea liebmannii and Orbignea sp.) (for detailed description of the vegetation communities in the study site, see Miranda 1952, 1961; Breedlove 1973; Calzada and Valdivia 1979; Meave del Castillo, 1983, 1990; Castillo-Campos and Narave 1992; Medellin 1992).

The second area is the Marques de Comillas Region (hereafter MCR) a fragmented forest landscape which includes patches of the vegetation described above, with few remnants of riparian communities. Most of this area has been converted into agricultural land for annual crops (e.g., corn, jalapeño pepper) (for more detailed on the deforestation process and land-use types, see De Voz 1980, 1988a, 1988b; Mauricio-Leguizamo 1984, O'Brien 1995, Arizpe et al. 1996). Using satellite imagery analysis, O'Brien (1995) estimated that between 1974-1979 and 1989-1992, the region lost 15,000 to 18,500 ha per year.

At the start of the breeding season, which corresponds to the beginning of the dry season (see Fig. 3-5 in Chapter 3) in late 1989 (November-December), January 1990, and January 1993, I searched intensively in MABR-LBR-YNP-SLNP-MBR and MCR for trees containing suitable cavities for use by Scarlet Macaws. I marked and plotted locations of the trees and simultaneously recorded all evidence of breeding behavior (e.g., nesting cavity guarding, copulation). These psittacines normally roost in pairs with their brood (1 or 2) in the interior of the cavities; consequently the entrance must be large enough to allow the bird to pass through without putting unnecessary pressure on the walls of the cavity entrance.

Presumed suitable nest-cavities were judged as being in either a snag or live tree at $\geq$ 10 m height from ground and with a nest cavity entrance of $\geq$ 0.15 m height $\bar{X}$ $\geq$ 0.15 m width. From such cavities the following information was recorded: (1) tree stage (dead or snag, live tree); (2) species of tree; (3) tree height, (4) tree diameter immediately above buttresses [note: height of tropical tree buttresses varies across species and individuals; (5) diameter of tree crown (m); (6) height to nest entrance; (7) tree diameter at nest; (8) nest cavity type (whether knothole at limb break, live branch, dead branch, on main trunk); (9) height of cavity entrance; (10) width of cavity entrance; (11) nest aspect (i.e., orientation of the hollow) recorded in 45° octants; (12) distance to main river; (13) terrain slope; (14) habitat type. At the Usumacinta drainage basin the cavity aspects (i.e., the direction towards a hollow opening) used by Scarlet Macaws during the breeding season (November-December 1989 and January-June 1990; and January-May 1993) were recorded and placed into eight equal compass classes with the major points as their centers (i.e., North, North-East, etc).

In both study areas (MABR-LBR and MCR), each potential nesting cavity was located with its latitude-longitude geographic reference system using a hand-held global position system (GPS) unit (Scout M GPS Trimble Navegation™). Cavities were examined every five days between November-December 1989, January-February 1990, and January-March 1993, when Scarlet Macaws search for cavities and lay eggs. Cavities which were used, were climbed and examined (every eight days) to follow reproductive activity and success after this, until occupancy terminated. In 1993 (January-May) each cavity was examined at an average of eight days at both the MABR-LBR-YNP-SLNP-MBR and MCR sites. In 1993 nesting cavities were observed from the ground at an average distance of 200 m from the nesting tree behind a blind. Each nest was observed an average of 20 times (once per week) for periods of 6-7 h each. To minimize bias associated with time of day, I alternated the order in which I observed each cavity between morning and afternoon. For example, in the first week of May I studied nest 1 from 0530 to 1130 h. The following week I observed the same nest in the afternoon from 1130-1730 h and the reverse order was followed the next week. Less intensive monitoring was conducted during 1989-1990 when each nest was surveyed every 10 to 15 days. Each nesting tree cavity and suitable cavities (as defined above) found in a transect were reached by using rock-climbing techniques (Perry 1978, Perry and Williams 1981) and measured.

I also studied the availability of suitable tree cavities not occupied by macaws in all trees with ≥ 1 m perimeter along three 2-km strip transects (50 m wide on either side of the transect center) in the continuous forest (MABR-LBR). I counted the number of suitable tress ≥ 1 m diameter and their cavities (at ≥ 10 m height from ground and with a cavity entrance of ≥ 0.15 m height $\overline{X}$ ≥ 0.15 m width) available at three 2-km strip transects. The same variables described above for nesting cavities were taken for these cavities.

## Results

### Macaws Searching for Cavities

Breeding Scarlet Macaws increase searching activity for nest cavities after the decline of the heavy rains (July-September) (see Chapter 3), and at the peak of fruit availability (Iñigo-Elias per. obs.) in the Usumacinta drainage basin during 1989-1990 and 1993. Macaws began to investigate different nesting cavities about a month before the breeding female's fertile period and they stopped searching when the clutch was laid. Approximately, three weeks before the clutch was laid, the breeding pairs became very vocal and began to focus their attention on a single nesting cavity.

In general, breeding macaw pairs intensified their search for nesting cavities during the months of January-March (Fig.4-1). During this period macaws searched for up to three cavities per day. Both parents simultaneously explored (i.e., look inside cavities) cavities. In a few cases (3 of 41 nesting attempts) both parents worked to enlarge the cavity by removing decaying wood with their bills and feet. One individual sometimes entered to inspect the cavity while the other remained outside, apparently guarding the cavity. Copulation frequency increased once a cavity was selected. Copulations occurred outside of the cavity on the nesting tree limbs or in nearby trees.

## Formation of Cavities

In the tropics tree cavities are formed at different stages and by various agents. Strong winds can break branches and the knothole created can become infected with fungi. Insects can also accelerate the formation of cavities. Cavities in the main tree-trunk are sometimes produced by other avian species such as woodpeckers.

In the study area, dominant winds and tropical storms bluster frequently from NE-E-SE directions (CILA unp. data). Of the trees and snags (n = 63) with potential cavities for macaws to nest (≥ 10 m height from ground; nest cavity entrance of ≥ 0.15 m height $\bar{X}$ ≥ 0.15 m width) found in the three strip-transects, only 19 (30%) of these cavities had the characteristics for macaws to nest.

Seventy-one percent of the broken limbs of a random sample (n = 31) of potential nesting cavity trees showed an orientation towards SW-W-NW-N and only 29% towards NE-E-SE-S. Knotholes were the most common cavity nest type with 76% (n = 41), followed by nesting cavities on live branches (13%) and nesting cavities on the main trunk (11%) (Table 4-1).

## Tree Species with Nest Cavities

The species of tree used as nest sites in both continuous and disturbed sites were pooled for analysis (Fig. 4-2). There were no preferences for either living trees or snags (Wilcoxon's Signed Ranks Test $Z$= 0.678, $P$ = 0.497). Snags ($n$ = 23) and live trees ($n$ = 18) were used as nesting sites in similar proportion. Only old trees are large enough to have cavities of suitable size for macaws.

Forty-one nesting trees were found and they belonged to eight different tree species. Three species of trees were used more often *Ceiba pentandra* (28.95%), *Schizolobium parahybum* (26.32%), and *Vatairea lundelli* (18.42%) than the remaining five species (Fig. 4-2). These species of trees were used in equal proportion to their occurrence in strip-transect (Test of Independence $G_{adj}$ = 0.010, df = 1, $P$ = > 0.05). These three tree species provided 73.69% of all nests sites and constituted 62.50% of all random trees (from the sample of suitable nest cavity trees) in strip-transects. *Ceiba* and *Schizolobium* appear to have a relatively soft wood compared to the other species in the area.

## Height and Perimeter of Nesting and Random Trees

I measured the height of 36 nesting trees and compared them to random trees ($n$ = 63). Random trees are those trees with ≥ 1m perimeter cavities within the three strip transects in MABR-LBR (Fig. 4-3a). Nest trees were taller than would be expected if birds selected trees solely on the basis of their availability (Wilcoxon's Signed Ranks Test Z = 1.997; P = 0.045). Thus Scarlet Macaws appeared to select taller trees in the study area. I also measured the diameters of 35 nesting trees and compared them to those random trees (n = 63) (Fig. 4-3b). However, random trees and cavity trees did not differ significantly in this aspect (Z = 1.261, P = 0.2071). Even though macaws nest more often in trees with 2-4 m perimeter (Fig. 4-3), this tree size is more frequent than other sizes.

### Random Tree Species and Suitable Cavities

Each transect was located perpendicular to the upper, mid, and low stream in the continuous forest site (MABR-LBR). In the upper river basin transect I found 16 suitable individual trees from seven species. In the mid river basin transect I found 32 suitable individual trees distributed in 10 species. In the low river basin transect I found 17 suitable individual trees from five species (Fig. 4-4). In the three transects *Licania platypus* is more common than other tree species and also has the most suitable cavities available (Fig. 4-4).

## Nest Cavity Height and Perimeter

I used a Pearson Product Moment Correlation analysis and found that nest cavity height was positively correlated to tree height ($r = 0.61$; $\underline{P} < 0.0001$; $\underline{n} = 35$; Fig 4-5a). Cavity entrance heights were extremely variable, ranging from 8.5 m to 51.6 m ($\overline{X} = 18.96$ m; SE = 1.37 m). Nest cavity height and tree perimeter were significantly correlated ($r = 0.39$, $\underline{P} = 0.022$; Fig. 4-5b). Nesting tree perimeters were variable, ranging from 1.5 m to 10.9 m ($\overline{X} = 4.36$ m; SE = 0.44 m).

Cavity entrance sizes were: height (range = 1.15 m to 0.15 m, $\overline{X} = 0.32$ m, SE = 0.040 m, Fig. 4-6) and width (range = 0.65 m to 0.12 m, $\overline{X} = 0.22$ m, SE = 0.023 m, Fig. 4-6). The height and width of the cavity entrance also were significantly correlated ($r = 0.84$, $\underline{P} = < 0.0001$, $\underline{n} = 25$, Fig. 4-6).

## Aspect of Nesting Cavities and Random Cavities

Most of the nests had an orientation towards N-NW-W-SW (66%) with others oriented to the S-SE-E-NE (34%) (Fig. 4-7a). Nests with cavities oriented towards the N-NW-W-SW had the highest percentage nesting success (i.e., more fledglings per nest). Occupied nest cavities did not differ significantly from the un-used cavities from the 63 trees in the three strip walking transects (Test of Independence $G_{adj}$

= 0.369, df 1, P = > 0.05) (Fig. 4-7a, b). Thirty-one trees of the three transects had more broken limbs with an orientation towards the N-NW-W-SW (71%;) than did to the S-SE-E-NE (29%) (Fig. 4-7c). Nest cavities oriented towards N-NW-W-SW were proportionally more similar than the unoccupied tree cavities and branches in random tree plots (Test of Independence $G_{adj}$ = 0.127, df 1, P = > 0.05; Fig. 4-7a, b, c).

A possible cause of branches breaking off may have been wind because the direction of storms in the study area was from SE-E-NE direction. These data show that macaws may use cavities oriented in opposite direction to the predominant rainy storms.

## Spatial Distribution of Nesting Tree Cavities

Nesting cavities occurred more often within 0-500 m of the edge of the river (90%, n = 41) than did random trees (56.6%, n = 60). An estimate of 7.5% of the nesting trees and 18.35% of the random trees occurred between 500-1,250 m to the edge of the river and 2.5% of the nests and 25% of the random trees occurred between 1,250 m to 2,000 m (Test of Homogeneity $G_{adj}$ = 15.28; P = 0.0001; df = 2; Fig. 4-8a, b). Vatairea lundelli and Schizolobium parahybum were found more commonly between 250-500 m from the edge of the river in both random trees (n = 63) and nesting trees (n = 36) (Fig. 7).

## Use of Cavities by Other Species

Other large secondary cavity nesters use hollows every year. These species include psittacines (Amazona farinosa, Amazona autumnalis), toucans (Ramphastos sulfuratus), falconiforms (Herpethoteres cachinnans), and strigiforms (Cicaba virgata). These species breed synchronously with Scarlet Macaws in the study area (Iñigo-Elias unp. data).

Bees (presumably Africanized because of their aggressive behavior towards macaws and researchers) were a serious problem during the study. During the 1993 breeding season, bees caused three of 41 active nests to fail (two with eggs alone and one with one egg and two fledglings). Bees usurped nesting cavities and swarmed into the top of the nest cavities in a matter of few minutes. Breeding pairs were attacked by the bees every time they approached the nest cavity. Around the world, bees commonly attack cavity nesting birds, particularly psittacines (Saunders 1979, Joyner 1994). Oldroyd (1994) found that psittacines and feral honey bees have an overlap of 48% in choosing cavities.

## Loss of Cavities

During this study five nesting cavities were lost due to strong winds that blew the trees to the ground. Two of these cavities had eggs. Most of these cases occurred during February 1990. Mature trees with cavities were particularly susceptible to winds.

Four nest trees were cut down by parrot poachers during the 1993 breeding season. I inspected the nests after they were cut down but could find no evidence of dead chicks, adults or crushed eggs. Presumably the poachers took the birds alive or dead.

In one case a nest snag was intentionally burned by a local person. Because we had the support of the whole community in the area, the responsible individual was sanctioned by the community and was forced to climb (approximately 15 m height) what was left of the snag and carve a new hollow to attract the breeding pair to return and nest. Amazingly the pair stayed nearby and re-nested, but not in the human-made cavity. Instead the pair created a new cavity on the top of the snag in what was an inactive woodpecker nest.

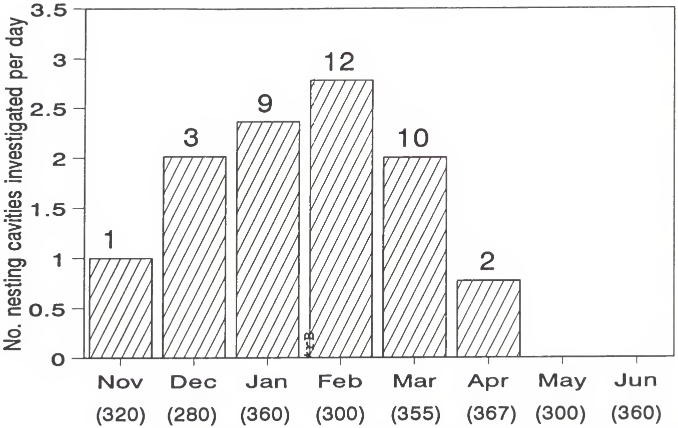

Figure 4-1. Average time Scarlet Macaws spend investigating a nesting cavity per day in the Usumacinta drainage basin of México and Guatemala during September-December 1989, January-August 1990, and January-May 1993 surveys. Number above bars indicate sample size (n). Numbers below months () are total number of hours of observation.

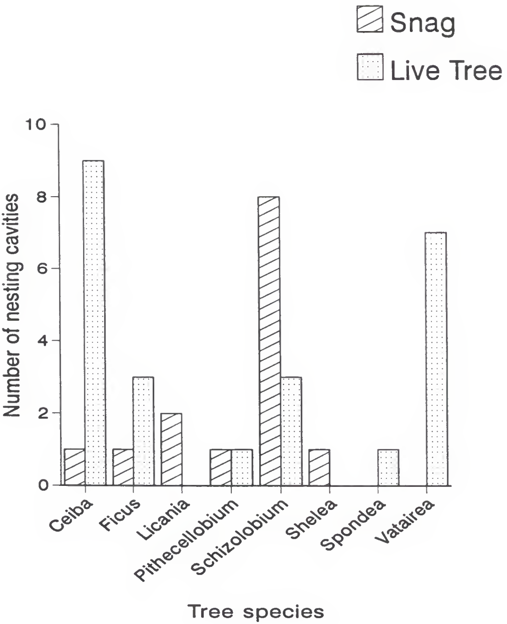

Figure 4-2. Average number of nesting cavities, investigated and occupied, by Scarlet Macaws per tree species in the Usumacinta drainage basin of México and Guatemala during September-December 1989, January-August 1990, and January-May 1993 surveys.

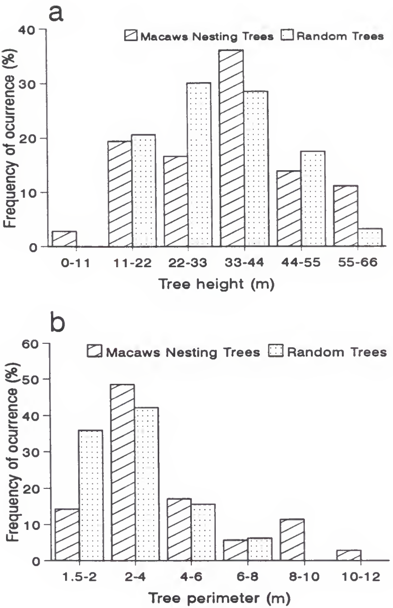

Figure 4-3. Frequency of occurrence in height and perimeter classes of 41 Scarlet Macaw nesting tress in relation to a random sample of 65 individual trees from different species with a perimeter ≥ 1 m in the Usumacinta drainage basin of México and Guatemala during 1989-1990 and 1993. a) Tree height frequency. b) Tree perimeter frequency.

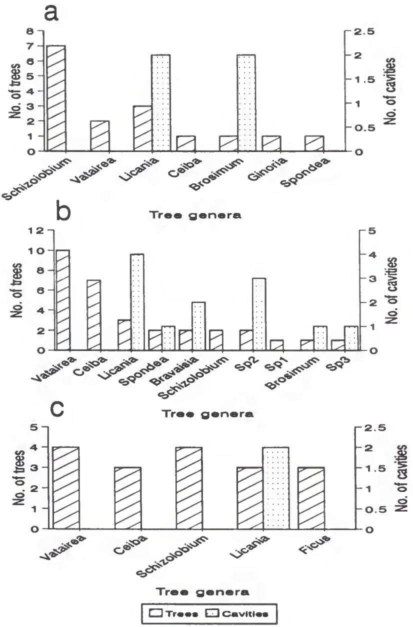

Figure 4-4. Number of trees by genera and cavities available of 65 random trees counted in three, 2-km long strip transects (100 m width). Each transect was located in either upper, mid, or low Lacantun river of México during 1989, January-August 1990, and January-May 1993 surveys. a) Upstream transect (Chajul). b) Midstream transect (Laguna San Leandro). c) Downstream transect (Tzendales).

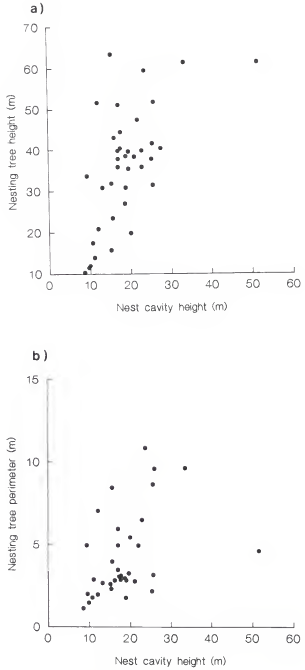

Figure 4-5. Relationship of a) nest cavity height (m) to nesting tree height (m) and b) nest cavity height (m) to nesting tree perimeter (m) for 41 Scarlet Macaw nests on the Usumacinta drainage basin of México and Guatemala during August-December 1989, January-August 1990, and January-May 1993 surveys. Data for live, dead, and decaying trees from both continuous and disturbed areas are pooled.

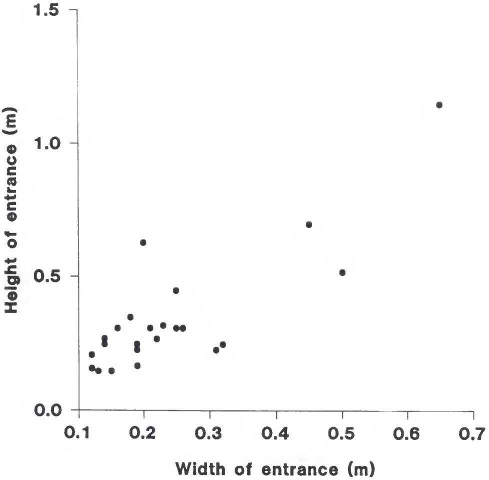

Figure 4-6. Relationship of cavity entrance width (m) to cavity entrance height (m) for 41 Scarlet Macaw nests on the Usumacinta drainage basin of México and Guatemala during August-December 1989, January-August 1990, and January-May 1993 surveys. Data for live, dead, and decaying trees from both continuous and disturbed areas are pooled together.

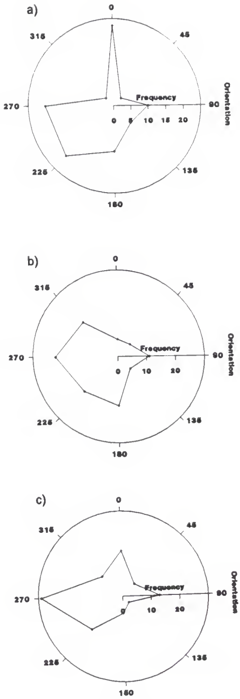

Figure 4-7. Frequency of the aspect (i.e., direction) towards which the entrance to a) the nest cavities used by Scarlet Macaws, faced ($\underline{n} = 41$), b) random cavities ($\underline{n} = 19$), and c) frequency of broken branch orientation ($\underline{n} = 31$) in the Selva Lacandona, region of Chiapas, Mexico during August-December 1989, January-August 1990, and January-May 1993.

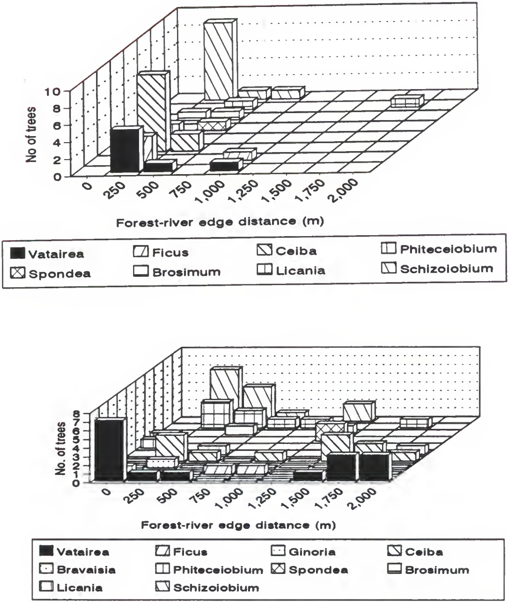

Figure 4-8. The distribution of a) nesting trees and b) random trees with respect to the edge of the Usumacinta drainage basin in México and Guatemala during August-December 1989, January-August 1990, and January-May 1993.

Table 6-1. Scarlet Macaw nest site and nest characteristics in the Usumacinta drainage basin of Mexico and Guatemala during 1989, 1990, and 1993. Al measurments are in m.

| Nest number | Nesting history | Tree stage | Tree height | Tree perimete | Nest height entrance | Height of entrance | Width of cavity entrance | Orientatio degrees | River distance |
|---|---|---|---|---|---|---|---|---|---|
| Ceiba pentandra | Succeed | live | 52 | 9.65 | 26 | 1.15 | 0.65 | 252 | 50 |
| Schizolobium parahybum | Succeed | dead | 31 | 2.7 | 13.1 | 0.63 | 0.2 | 229 | 20 |
| Schizolobium parahybum | Fail | dead | 14 | 2.9 | 11 | 0.7 | 0.45 | 262 | 25 |
| Vatairea lundellii | Abandon | live | 38.7 | 2.87 | 19 | * | * | * | 13 |
| Ficus sp | Succeed | live | 51.8 | 7.1 | 12.1 | 0.25 | 0.14 | 18 | 72 |
| Spondea sp | Succeed | live | 27.1 | 3 | 18.66 | 0.21 | 0.12 | 226 | 378 |
| Ceiba pentandra | Succeed | live | 61.6 | 9.7 | 33.6 | 0.35 | 0.18 | 181 | 120 |
| Ceiba pentandra | Succeed | dead | 31.6 | 8.7 | 25.6 | 0.31 | 0.26 | 277 | 150 |
| Ceiba pentandra | Abandon | live | 63.6 | 8.5 | 15.6 | 0.25 | 0.32 | * | 300 |
| Schizolobium parahybum | Fail | dead | 23.6 | 4 | 15.6 | * | * | 298 | 250 |
| Schizolobium parahybum | Fail | dead | * | * | * | * | * | * | 15 |
| Schizolobium parahybum | Fail | dead | * | 3.7 | * | * | * | * | 250 |
| Ceiba pentandra | Succeed | live | 59.6 | 10.9 | 23.8 | 27 | 18 | 318 | 200 |
| Pithecellobium leucocalyx | Fail | live | 38 | 6 | 17 | 17 | 15 | * | 50 |
| Ceiba pentandra | Fail | live | 20 | 5.5 | 20 | * | * | * | 40 |
| Schizolobium parahybum | Succeed | live | * | * | * | * | * | * | 600 |
| Ceiba pentandra | Fail | live | * | * | * | * | * | * | 300 |
| Pithecellobium leucocalyx | Succeed | dead | 17.6 | 1.8 | 10.6 | 30 | 18 | 310 | 300 |
| Schizolobium parahybum | Fail | dead | * | * | * | * | * | * | 270 |
| Vatairea lundellii | Abandon | live | 40.6 | 2.9 | 17.6 | 0.15 | 0.15 | 122 | 1000 |
| Vatairea lundellii | Abandon | live | 35.6 | 3.3 | 19.6 | 0.15 | 0.13 | 309 | 350 |
| Ceiba pentandra | Succeed | live | 39.8 | 3.3 | 19.6 | 0.15 | 0.13 | 309 | 250 |
| Licania platypus | Fail | dead | 38 | 2.2 | 25.3 | 0.31 | 0.25 | * | 200 |
| Vatairea lundellii | Abandon | live | 41.8 | 3.2 | 25.6 | 0.27 | 0.22 | 120 | 150 |
| Ficus sp | Fail | live | 31 | 1.8 | 18.9 | 0.25 | 0.19 | 45 | 250 |
| Ficus sp | Abandon | live | 36 | 3.5 | 17 | * | * | 124 | 250 |
| Ceiba pentandra | Fail | live | 21 | 2 | 12 | 0.27 | 0.14 | 184 | 100 |
| Vatairea lundellii | Fail | live | 61.6 | 4.65 | 51.6 | 0.31 | 0.16 | 42 | 50 |
| Vatairea lundellii | Fail | live | 40 | 5 | 17 | 0.32 | 0.23 | 44 | 30 |
| Ficus sp | Succeed | dead | 33.85 | 5 | 9.35 | 0.16 | 0.12 | 286 | 800 |
| Schizolobium parahybum | Succeed | live | 51.3 | 3.1 | 17.2 | 0.31 | 0.21 | 32 | 16 |
| Schizolobium parahybum | Succeed | live | 44.6 | 3.15 | 17.71 | * | * | 220 | * |
| Schizolobium parahybum | Fail | dead | * | * | * | * | * | * | * |
| Vatairea lundellii | Abandon | live | 32 | 2.35 | 15.3 | 0.52 | 0.5 | 23 | 31 |
| Ceiba pentandra | Succeed | dead | 40.6 | * | 27.6 | 0.45 | 0.25 | 261 | 250 |
| Licania platypus | Fail | dead | 38.6 | 2.8 | 21.1 | 0.23 | 0.19 | 177 | 300 |
| Shelea sp. | Abandon | dead | 12.1 | 1.5 | 9.85 | 0.17 | 0.19 | 161 | 800 |
| Schisolobium | Abandon | dead | 15.85 | 2.64 | 15.1 | 0.15 | 0.13 | 254 | 200 |

# CHAPTER 5
# BREEDING BIOLOGY OF THE SCARLET MACAW IN THE USUMACINTA DRAINAGE BASIN OF MEXICO AND GUATEMALA

## Introduction

Little is known about the breeding biology of the Scarlet Macao (Ara macao) (Family Psittaciadae, Order Psittaciformes) in the wild, one of the 13 extant species of the Neotropical genus Ara. Scarlet Macaws inhabit riparian and lowland tropical evergreen and semi-evergreen forests as well as landscapes with agricultural fields and forest remnants (Ridgley 1982, Forshaw 1989, Munn 1994, Iñigo-Elias in prep.). In Mexico and Central America most of the Scarlet Macaws nest during the dry season, November to late May (Kainer 1991, Iñigo-Elias pers. obs.) whereas in Peru and Brazil they start nesting at the end of the dry season (August-October) and fledglings leave the nest at the end of the rainy season (April-May) (Roth 1984, Munn et al. 1991). In recent years more information has been published on the biology and ecology of wild macaws (Marineros 1993, Munn 1994, 1995; Bjork and Powell 1995; Marineros and Vaughan 1995; Nycander et al. 1995).

The Scarlet Macaw is a species of great concern because it has declined drastically in México and North Central

America in the last 30 years because illegal harvesting for both local and international pet trades and habitat destruction. México and several countries in Latin America have expressed on different occasions their interest in "sustainable harvest" or "ranching" of Scarlet Macaws and other parrots. Modelling for the harvest of wild macaws requires: (1) to have a very detailed life history (i.e., reproductive rate, age at first reproduction, reproductive risk, mortality, emigration, and so on) of a particular macaw population (2) a known population that is sufficiently large; (3) a careful design and vigilance during the harvesting process to eliminate all possible loopholes for illegal activities and smuggling of birds. Once this information is collected sustainable harvesting may be implemented.

In this chapter I describe the breeding biology, particularly nesting behavior, egg and incubation, nestlings growth and parental care, of the Scarlet Macaw. I observed macaw breeding behavior during the breeding seasons of 1989, 1990 and 1993 along the riparian forests of the Usumacinta drainage basin of México and Guatemala.

## Materials and Methods

I studied Scarlet Macaws in the riparian forests and agroecosystems in a study area of a 52,000 ha at 138 m along the Usumacinta drainage basin (including the Jataté, Ixcán, Chajulillo, Miranda, Lacantún, Lacanja, Aguilar, and Usumacinta Rivers). This study covered two breeding seasons, 1989-90 and 1993. The study area was comprised of two main vegetation and land use types, a continuous forest, and a disturbed landscape divided by the Jataté, Lacantún and Usumacinta rivers (see Chapter 4 for more details).

The climate of the Usumacinta drainage basin is characterized by three main regimes: (1) hot-humid with summer rainfall and scattered winter rains with the driest month having less than 60 mm of precipitation which are from December to late May; (2) semi-hot with a mean annual temperature lower than 22°C and the coldest month of the year with a greater temperature of 18°C; and (3) hot-humid with rainfall all year long with two rainfall peaks during the year, one in June to July and in September to October (mean annual rainfall ≈ 2,500 mm, range 1,000-5,000 mm), the driest month having more than 60 mm of precipitation (CETENAL 1974; CILAc 1987; Meave del Castillo 1983, 1990).

The region was exhaustively searched on foot and by boat transects as well as by aerial surveys (Cessna Airplane with 2 observers) for nesting attempts (see Chapter 3). I also interviewed several former macaw poachers. My two assistants and I investigated any potential nesting site from the first day of detection until any breeding activity ceased (e.g., breeding pair abandoned the site, fledglings and parents left the site). I made observations of each nesting attempt from an average distance of 300 m with the aid of a telescope (15-45 x 60) and binoculars (10 x 42). Each nest was observed weekly for a period of 6-7 h either in the morning (0530-11:30) in the afternoon (1200-1800). Morning and afternoon observation periods of each nest were alternated weekly to reduce bias related to time of day. In my study area sundown occurred approximately at 1800 h throughout the year.

To reduce stressing the mating parents, I climbed each nest tree only when the parents were absent (Gotmark 1992). The parents typically left the nest early in the morning and I observed most of them searching for food and or stretching their wings along 200-500 m away from the nesting tree. I climbed only accessible nests (i.e., not in a snag) using rock climbing techniques (Perry 1978, Perry and Williams 1981) to inspect the clutch or nestling(s) condition. When I found eggs I measured the length and width (mm) as well as the weight (g). When nestlings were found I measured: (1) length of exposed culmen without cere (mm); (2) length of closed wing (mm); (3) length of tail (mm); (4) length of tarsus (mm); and (5) weight (g). Measurement procedures followed Baldwin et al. (1931). I wore disposable surgical gloves and disposable organic vapor/dust mist respirators (Pel $< 0.05$ mg/m$^3$) when handling eggs or nestlings at each nest to reduce the risk of passing diseases from nest to nest and from the birds to the investigator and vice versa (suggested by C. Munn, pers. com).

I measured and weighed eggs and nestlings found in only seven nests in Mexican territory every five to eight days as permitted by the Direccion General de Conservación de los Recursos Naturales (SEMARNAP). I was limited to studying just seven nests to reduce desertion by breeding pairs. Scarlet Macaws are legally protected by both Mexican and Guatemalan laws as endangered species and are included in Appendix I of CITES (Ramos 1985, Schouten 1992, Diario Oficial 1994).

## Results

I spent 1,950 h observing the breeding behavior of Scarlet Macaws from January 13 to May 31, 1993 in the Usumacinta drainage basin. Here the macaws are non-migratory. Scarlet Macaws spend most of their time in the tree canopy. Even though there are several clay walls along the Usumacinta drainage basin, these are not leaking clays such as those that psittacines visit in the Amazon region of Peru (Munn 1994). Scarlet Macaws are monochromatic and juveniles can only be detected by their dark iris. I was able to recognize breeding pairs by the presence of the female's brood patch. Additionally, the breeding pair was distinguishable because during the incubation period females lost between 30% and 90% of their central rectrices and males did not. Also males developed a large dark brown spot on their breast plumage as a result of regurgitating food to the female. Males gradually lost the tail feathers during the nesting cycle.

## Mating System

At the Usumacinta drainage basin macaws behaved as those in other parts of the Neotropics and in captivity, they were monogamous and live year round in pairs. Breeding or not, most pairs defended their nesting sites from conspecifics or individuals of other species (e.g., *Ramphastos sulfuratus*, *Herpethores cachinnans*). During the study I observed 41 nesting attempts (i.e., any activity such as nest construction, copulation, presence of eggs or brood). On these I observed seven instances when macaw pairs guarded their potential nest cavity through the nesting cycle, yet showed no evidence of any other nesting behavior. In these nests no copulation nor eggs or nestlings were found. Breeding or not, most macaw pairs spent the night together inside the cavity.

## Annual Breeding Cycle

Scarlet Macaws annual breeding cycle in the Usumacinta drainage basin coincides with the driest months of the year. Of the total nesting attempts (n = 41), I found only eleven of them on eggs. These breeding pairs began incubating between the last two weeks of December and the second week of February (n = 11) and the eggs hatched about 35 days later, in the driest period of the year (March). Fledglings left the nest with their parents in the first rains, in late May or early June (Fig. 5-1, 5-2). The beginning of the breeding season was characterized by several changes in Scarlet Macaw behavior and feather conditions: (1) investigation of nesting cavities intensified by pairs; (2) intra- and inter-specific defense of potential nesting sites; (3) copulation attempts on the nest tree or nearby; (4) individuals I believed were males began to provide food to the presumed females; (5) females increased the size of their brood patches; (6) female central (longest) rectrices began to bend and then break completely; and (7) male breast and throat feathers began to change color from bright red to dark brown as a result of passing food to the female. I began to investigate cavities in mid-November (1990) and early January (1993), just after the peak of the rainy season (Fig. 5-2).

Copulations became more frequent during the months of January and February. During the breeding season of 1993, of the 41 nesting trees I observed 13 pairs copulating during January and February but only 2 pairs in March. This process continued slightly during incubation and declined after hatching. After the clutch hatched, copulations occurred infrequently. During incubation and after hatching, males offered food to the females 3-4 times a day. I never observed males passing food to the newly hatched nestlings. Males always transferred food to the females out of the nest or in the nest cavity lip.

## Mating Behavior

Scarlet Macaw copulation attempts were generally preceded by a short period of solicitation (soliciting mate raised its tail), at least when they were not disturbed by other species, people, or other macaws. Copulation attempts observed in 15 nests ranged from 3 to 15 seconds ($\bar{X} = 7.9$) and were initiated after long allopreening periods. After this macaws took a flat body posture, close to the branch and increased the frequency of calling. Copulation occurred side-by-side either facing the same or opposite direction ($n = 27$; in 19 nests). Both male and female defended the nest from conspecifics and other birds. On one occasion I saw four macaw pairs simultaneously try to take over an active macaw nest with fresh eggs. The female stayed in the cavity entrance with the wing and tail feathers opened, while the male attacked the macaws flying over the nest entrance. On two occasions the defending male almost hit the ground with the attacking bird. The breeding pair was successful in chasing out the attackers.

## Nesting Sites

Scarlet Macaws in my study area laid eggs (clutch size = 1-3) in preexisting cavities elevated in tress or snags (Fig. 5-1). Nesting cavities received little preparation by both parents, who cleaned the cavity floor by removing debris with their bill or by kicking debris from the cavity (e.g., feathers, bones, insects). During December to late January, I observed macaws cleaning nests (n =11). In most cases both parents had wood chips on their breast feathers indicating that both parents participated in the cleaning. I observed on one occasion a female kill and discard an *Anolis sp*. lizard from the interior of the nest when both parents were clearing debris from the nest cavity. Scarlet Macaws never built a nest, instead they laid their eggs directly on the floor of the cavity. The cavities' floors were either flat or slightly concave and consisted of a thick (10 cm) layer of well-packed, decayed wood overlaying a more solid wood base. Macaw contour feathers were rarely found in the nest. Cavity depths varied from 1.5 m to 0.25 m from the entrance to the nest bottom (*n* = 19) (see Chapter 4 for more information nesting site characteristics and cavities).

## Egg Incubation

I found five fresh fertile eggs in tree nests (clutch sizes = 1, 2, and 2); these were monitored daily during the incubation period. Scarlet Macaw eggs are white, semi-round, and have a smooth texture. Eggs had an average length of 44.8 ± 1.38 mm and an average width of 35.6 ± 0.68 mm (n = 5 eggs, in 3 nests). The average mass of freshly laid Scarlet Macaw eggs was 33.39 ± 0.94 g. The average clutch size in the study site was 1.57 (n = 11) range 1-3, with a mode of two. While laying the clutch, females spent between 76% and 92% of their time inside the nest. Males returned to nest and fed the female four to six times a day. The passing of food from male to female occurred mainly outside the cavity but in the same nesting tree (85%) as well as in the nest entrance (15%). There were no incubation shifts; females exclusively incubated, as is the case in captivity (Abramson et al 1995). During incubation females only stopped incubation (i.e., perching on nest cavity lip, fly outside of nest cavity to stretched wings), between 8 to 13 times a day for an average period of 7.6 minutes (n = 11 nests for 7 h observation periods, January-May 1993).

## Nestlings and Fledglings

Scarlet Macaw nestlings are altricial and hatched (i.e., incubation length) after 28-34 days (n = 9) (Fig 5-2). In 87% of the nests, both eggs hatched. The two nestlings of known age had masses of 24.6 and 27.3 g a few hours after hatching.

Nestlings were probably most vulnerable to attack or predation in the early days of life. During this time nestlings relied on adults for protection. Prior to fledging, they spent several minutes a day showing their heads out of the cavity. Mass of nestlings increased steadily during the first 50 days of age (Fig. 5-3). Between 80 and 90 days of age, weaning (process by which birds learn to eat on their own) occurred and the chicks began to lose weight. Mass loss seemed to stabilize after about 90 days (Fig. 5-3.a.). Wing length was a more steadily rising curve (Fig. 5-3.b). In my study most of the fledglings abandoned the nest at an age of 65 to 75 days and became independent at an age of 80 to 90 days.

## Nest Attendance

As egg laying and incubation progressed female Scarlet Macaws increased their nest attendance (Fig. 5-4) and spent only brief periods away from their nests. I found little variability among nests. Figure 5-5 shows the mean and SE of nest behavior pooled data ($\underline{n}$ = 11) for females. Females reduced nest attendance below 50% of the nest attendance after the nestlings were 75 to 85 days old. At the end of the nestling cycle, however, females decreased their attendance (Fig. 5-4), spending less time (20% or less) than early in the breeding season. Males only entered the nest at dusk. During early nestling rearing, 40-60 days, males became less attentive to the nest and spent more time apparently in search of food or stretching. They also visited the nest more often with food, approximately five to nine times per day.

## Nest Predation

Feral bees posed a serious threat to macaws. During the 1993 breeding season, bees caused three of 41 active nests to fail (two with eggs alone and one with one egg and two fledglings). Breeding pairs were attacked by the bees every time they approached the nest cavity. Additional predation problems occurred with falconiform and strigiform species that preyed on nestlings. In one nest I observed during the 1989-1990 season a Bat Falcon (*Falco rufigularis*) killed and ate a new Scarlet Macaw nestling. I presumed the Bat Falcon was going to take over the nest cavity but it was attacked and driven off later by the Scarlet Macaw nesting pair (Iñigo-Elias in prep.).

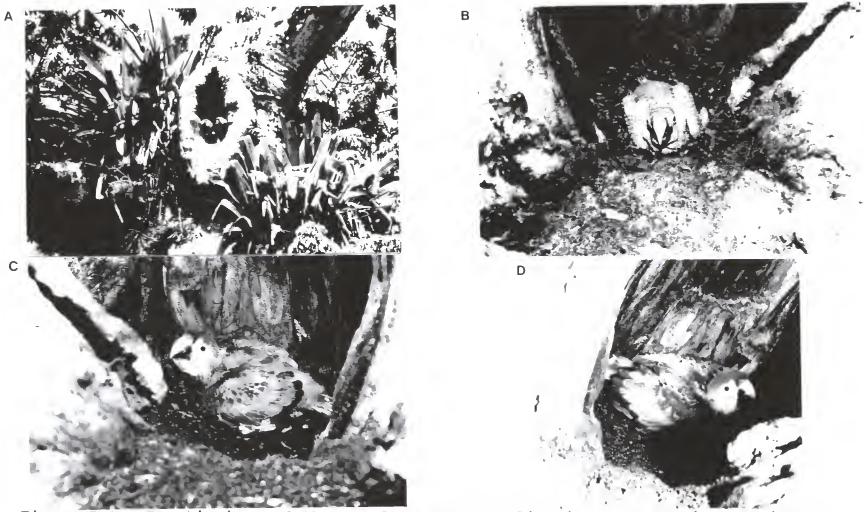

Figure 5-1. Frontispiece of the Scarlet Macaw nestling in the Usumacinta drainage basin of México and Guatemala. a) Scarlet Macaw egg and two day old nestling in enclosed nesting cavity in trunk of a live tree (*Ficus* sp.). b) Down-covered Scarlet Macaw nestling two weeks after hatching. c) Scarlet Macaw nestling about 6 weeks after hatching. d) Scarlet Macaw nestling 10 weeks old.

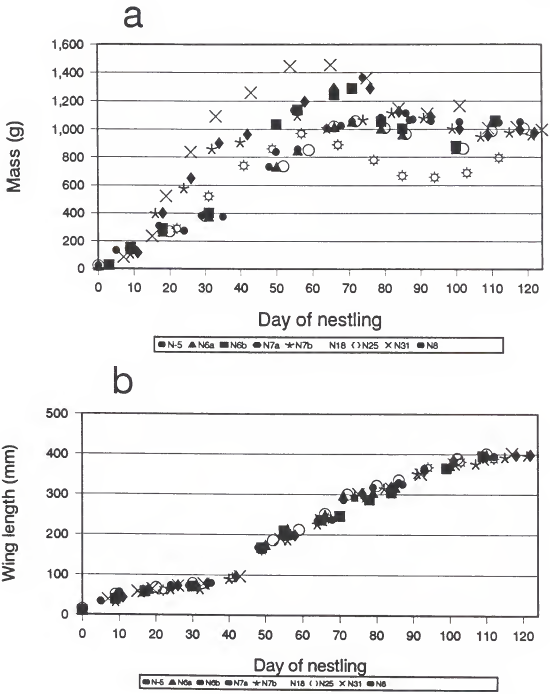

Figure 5-2. Growth curves of wild Scarlet Macaw nestlings in the Usumacinta drainage basin of México and Guatemala during the 120 day nesting cycle. Measurements of 9 nestlings from 7 nests taken early in the mornings (06-07 h) after parents flew for food or to stretch in the Usumacinta drainage of México and Guatemala from January-May 1993. a) Increase in mass (g) and b) Wing length (mm) flattened.

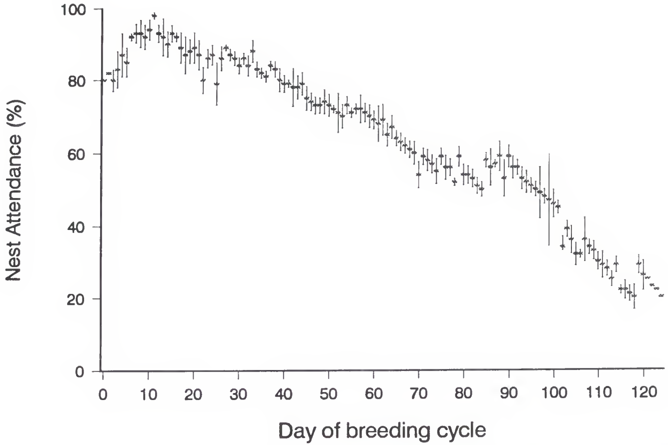

Figure 5-3. Time budget for nesting attendance by female Scarlet Macaw in the Usumacinta drainage basin of México and Guatemala. Nest attendance represents percentage of a 7-h period (AM or PM) spent by ♀ at the nest cavity.

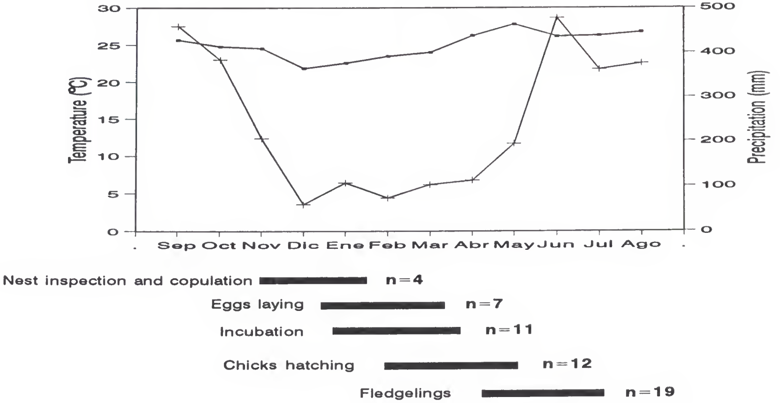

Figure 5-4. Breeding cycle in Scarlet Macaws related to mean rainfall (+--+--) and temperature (.--.--.). Climatological data from stations along Usumacinta drainage basin during 1993.

# CHAPTER 6
# DISCUSSION AND CONCLUSIONS

## Comparison of Walking and River Surveys

The extreme difficulty of observing macaws in their natural surroundings has prevented field biologist from being able to study their breeding biology in the wild. My observations on Scarlet Macaws (*Ara macao*) provide new insights into census techniques and population biology (i.e., the study of the spatial and temporal distribution of organisms) on a tropical riparian landscape in the Usumacinta drainage basin of México and Guatemala.

Line transect techniques may be very useful for studying birds in forested areas where visibility is limited and walking surveys are often the only feasible method (Emlen 1971, Järvinen and Väisänen 1975, Karr 1981, Harden *et al*. 1986, Brockelman and Ali 1987, Ornelas *et al*. 1993).

It was clear from the data that visual records were the best way to detect Scarlet Macaws. Even though Scarlet Macaws are highly vocal, their red color makes them very conspicuous and easy to detect visually before they call. Moreover, aural detections still are not very useful when counting macaws in thick forests because the number of birds in a flock cannot be counted. Karr (1981) suggested that tropical forest species have different behaviors than temperate forest birds and natural history attributes that significantly affect census accuracy. Furthermore, several physical and biological factors reduce the precision of count surveys in tropical environments. Among the most notable are weather (e.g., rainfall and wind), topography, and vegetation structure (Karr 1981, Oelke, 1981, Bibby et al. 1992).

In the continuous forest (MABR-LBR), the vegetation structure was more homogeneous than in the disturbed forest (MCR) where the vegetative associations were very complex and macaws used more diverse habitat strata. It is clear from the data that Scarlet Macaws tended to use the canopy strata more than other strata in both MABR-LBR and MCR.

According to the results of this project it is more appropriate to survey macaws during the morning hours than in the afternoon. Because biases of counts differentially affect macaw detections (and may skew the representation of sexes and ages too), and because biases differ across seasons and habitats, it is very risky to assume that we can properly compare species populations across time scales (seasons or years) or across different habitat types.

The slight differences of the total densities of Scarlet Macaws in the continuous (3.86 macaws/Km$^2$) versus the disturbed forests (5.80 macaws/Km$^2$) may have been a result of greater vegetation structure on the continuous forest that reduced the detectability of birds.

## Nesting Sites and Nesting Cavities

The increase of deforestation in tropical forests (Gomez-Pompa et al. 1972, Ehrlich 1988, FAO 1993, Arizpe et al. 1996), the destruction of nesting cavities and trees by parrot poachers (Iñigo-Elias and Ramos 1991, Enkerlin-Hoeflich 1994, Munn 1994) have shown a decline in the availability of nesting sites as well as macaws (Munn 1988, 1991; Iñigo-Elias in prep.). Gibbs et al. (1993) suggested that limitations of nesting cavities could be more severe in tropical environments than in temperate forests. Some of the evidence they provided for nesting cavity limitation included: (1) low density of snags (i.e., standing dead trees) in tropical and subtropical forests (3.5-20.5 snags/ha) compared to temperate forests (21.2-49.3); (2) increased number of cavity nesting bird species in tropical forests (X = 33.6 ± 12.3) than in temperate forests (X = 14.8 ± 5.2); and (3) relatively fewer cavity excavating species in tropical forests.

The supply of adequate numbers of cavity-bearing trees in perpetuity for wildlife requires the retention of both cavity-bearing trees and a supply of younger trees to replace the older trees as they are lost through natural processes or human activities. There is a need to conduct extensive studies on the dynamics of formation of tree cavities and community ecology of secondary cavity nesting birds.

Although some macaws breed in fragments or in isolated trees in pastures, they are not likely to do so in the future, because much of this remnant woodland is mature, and exposed to damage by strong winds and fires. Scarlet Macaws have a better chance of surviving in large tracts of forest where suitable cavities are more common than in open and small forest remnants. Destruction of nest cavities by poachers, the occupation of cavities by expanding populations of Africanized bees, and the effects of clearing for agriculture, ensure that cavities are being destroyed faster than they are being formed.

Conservation and management programs with this species in México and Central America should study first the macaw population size and the availability of nesting sites. Further management strategies could include monitoring programs with artificial nesting boxes. These types of studies should be conducted with a rigorous experimental design to sample the effects of cavity nests on the macaw population before and after the implementation of nesting sites.

The use of nesting boxes offers the alternative to study with more detail the breeding biology of the species because boxes can be searched more frequently and easily than natural cavities. Also nesting boxes can be used as a conservation tool with rural communities by establishing community-based programs where communities could protect nesting sites. After clearing the forest, disturbed agroecosystems (e.g., forest fragments with edges of cacao plantations, forest fragments with edges of pastures) in MCR contained some nesting cavities. Census for potential nesting trees and cavities in the forest area of MABR-LBR led to the formation of the hypothesis that macaws may be limited by nesting cavity availability. Suitable nesting cavities for macaws are not abundant in my study site, or in Costa Rica (Marineros and Vaughan 1995), Peru (Munn 1988), and Brazil (Guedes and Harper 1995).

Scarlet Macaw nests in the Usumacinta drainage basin of México and Guatemala do not show clear differences in site characteristics. For the nest-site parameters where significant differences occurred, they were slight and range values overlapped frequently. However a multivariate analysis of variance might reveal significant differences between used and unused cavities. Such a test may require larger sample sizes. In this study, three species of trees, Ceiba pentandra, Schizolobium parahybum, and Vatairea lundelli, were most frequently used by Scarlet Macaws but nests were found in five other tree species. Most nesting cavities faced towards N-NW-W-SW octants and few towards the S-SE-E-NE. This led to the formation of the hypothesis that

Scarlet Macaws were using any nesting cavity with any octant aspect available. Non-nesting cavities and broken limbs showed similar orientation as nesting cavities. This suggests that macaws are merely using what is available in nature and not selecting for any orientation. One explanation for why cavities tended to form with such an orientation is that winds and storms in the study site predominantly advanced from the NE-E-SE direction, inducing pressure at the base of the branches facing perpendicular to the wind.

Macaws used any cavity available without selecting for any particular feature of the cavity (e.g., orientation). Macaws bred in nest sites with clear understory possibly to reduce predation rates.

In both forest and disturbed agroecosystems, macaws bred successfully. Productivity and chick survival of Scarlet Macaws in the study site were also observed. Macaws were able to raise two chicks in nests not that were disturbed. Nest predation was high, approximately 58%, both natural causes and poaching of nestlings were also major factors. It is possible that the habitat in the study site represents a marginal area for Scarlet Macaws. Since it lies at the northern edge of the historical range. However, it may be the best remaining habitat in Mexico for Scarlet Macaws.

Two determine the magnitude of the influence of current illegal harvesting activities on parrot populations, it is critical to document the balance between adult mortality and recruitment of new pairs into reproductive segments of the population. Since both variables require long-term study, I focused on measuring productivity in terms of determining clutch size and mortality prior to fledgling. Causes of mortality prior to fledgling also are important in assessing whether human harvesting is additive or compensatory relative to natural causes of mortality. The low productivity of Scarlet Macaws in my study may be cause for concern, since this is the one of the most desirable species in the pet trade. Currently the state government of Chiapas and some rural communities in the region are interested in developing a "sustainable harvesting" program of macaws in Mexico. The results presented in this research project show that the Scarlet Macaw population of Southern Mexico is in danger of extinction. A program to harvest macaws will increase the risk of extirpation of the species in Mexico territory as well as in Guatemala. Furthermore, a management program for harvesting macaws require a long-term data base of life tables that can be used to estimate the appropriate levels of harvesting. Such program may never be sustainable. Further biological research, management programs, and protection of the species and nesting sites is urgently required in the region to recover the species.

Continuation of studies of this population may clarify several important characteristics. Philopatry of young birds, if present, would allow for the application and evaluation of site-specific management. If harvesting schemes are implemented in the future, increased density of nesting birds due to philopatry would directly benefit land owners applying appropriate management practices.

## Breeding Biology

The extreme difficulty of studying Scarlet Macaws in the field has prevented scientists from being able to collect accurate and sufficient information on the life history of most psittacine species. Moreover it may hamper the use of experimental methods.

Scarlet Macaws that successfully raised their young exhibited distinct patterns of nesting behavior during incubation and early nestling rearing. During egg laying and incubation females in successful nest maintained high nest attendance periods with only brief recesses. These Females spent less time in the nest cavity as nestling rearing progressed (Fig. 5-4). Males entered the nest more often as nestling rearing progressed.

These distinct patterns of behavior reflect the importance of the incubation and early nestling-rearing periods to successful reproduction, as eggs and young nestlings are vulnerable to predation, temperature extremes, and variation in humidity.

Behavior of female macaws during early nestling rearing reflects the changing thermoregulatory and nutritional needs of their young. Captive females maintain high nest attendance while nestlings are dependent on almost constant brooding for survival (Abramson et al. 1995). Extended absences at this time can expose the nestlings to chilling temperatures and leave them too weak to beg for food, thus increasing their susceptibility to diseases. Prolonged exposure to low temperatures may also cause poor digestion and may decrease growth rates (Abramson 1991, 1995a, 1995b, Clubb et al. 1992).

On several occasions I observed conspecific attacks of macaws for nesting cavities. These observations combined with the in Chapter 3 and those of Munn (1991, 1994) show that nesting cavities can be a resource that limits the abundance of breeding pairs in the study area. Suitable nesting cavities are scarce.

## Management and Conservation

The prospect of harvesting macaws to sustain both domestic and international pet trade are very bleak with the Mexican and Guatemala population along the Usumacinta drainage basin. In this research I found that the total breeding population of Scarlet Macaws in the region is probably less than 200 breeding pairs. Poaching is a persistent problem and in many instances poachers cut down the nesting trees to reach the brood of macaws. If nestlings survive the crash the may die later because of broken bones or their injuries, or from poor care. Macaws tend to defend nesting cavities from conspecifics. Observations of direct combat between pairs of macaws searching for nesting cavities with macaws "setting" in the interior of cavities during the breeding season without showing any breeding behavior (e.g., copulation) suggest that in the study site Scarlet Macaws have a strong degree of philopatry (site fidelity) and may nest every two years (Munn 1988, Iñigo-Elias in prep).

Ranching of wild macaws has several problems:

(1) macaw populations may never reach an adequate levels because they have a low reproductive rate (1-2 eggs), long reproduction, slow nestling growth, and high mortality. (2) It is possible that wild macaws nest only every two years (Munn 1988, Iñigo-Elias unp. data). As I described in Chapter 5 seven macaw pairs guarded a tree cavity throughout the nesting season yet never copulated or laid eggs. (3) If one of two nestlings is removed from a wild nest how do we know that we have left a healthy bird with its parent? (4) If fresh eggs are removed from a nest the stress that we may produce on the breeding pair could be so high that the macaws abandon the nest and not breed that year. The

affected or parents may lay laid a second clutch with less "healthy nestlings" and with much lower probability of survival. (5) If we removed eggs from wild macaw nests we may push parents to nest and have fledglings late in the breeding season who may have less food available than earlier nesting birds, again reducing chances of successful reproduction.

All these factors should be take into consideration before any harvesting program of macaws is proposed or implemented.

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# BIOGRAPHICAL SKETCH

I was born in June 12, 1960, in México City. My parents, Ernesto and Liliana, both were born in Mexico but their relatives were immigrants from the Vasco Province from Spain and from Lebanon that arrived in México a long time ago. I came from a family of five children, but I was the only one to develop a personal strength for geology, paleontology, biology, and of course ornithology. During my first two years of life I grew up surrounded with tropical fishes that my father, a journalist, raised as a hobby. My mother taught me the names of all the birds that I saw in Mexico City, Chapultepec Zoo, and with the "pajareros" (bird dealers) that walk around the streests of D.F carring on their back a column of cages with wild caught birds. During my childhood both of my parents motivated me to maintain an interest in wildlife. They and my uncle Eleazar and Margarita influenced me by giving me natural history books and by being gentle. Nevertheless, when I started college they disapproved of my being a field biologist they instead wanted me to have a carreer as an M.D. or Marine Geologist from the Mexican Navy School. I am glad I did not listen to them!

My grandfather, a train engineer, was one of my favorite childhood heros who told me many stories and describe exciting landscapes he experienced when he was guiding steam locomotives (e.g., Baldwin B-8 [1892]; Al Co Cooke G-18 [1903-1908]; Al Co. Baldwin "Niagara" QR-1 [1946-1962] across México. He encouraged my interest in steam locomotives, frontier exploration, and rural México.

As a boy, six to 12 years old, I used to climb the walls of my third floor house and watch the breeding cycle of the House Sparrow (Passer domesticus) for hours as they nested in the holes between the bricks. Around the same time my brother and many of my friends from "Violetas" street joined the 89 Boy Scout Troop until 1976 we explored and camped in many forest areas of México. I ran into many troubles with my troop leaders because I disappeared for hours when I was watching birds, rocks, streams, and plants. During these wonderful times I developed a strong interest in natural history.

I went to college at Mexico's Universidad Autónoma Metropolitana - Iztapalapa (UAM) where I learned ecology and disliked human neurophysiology and final tests. After college I joined the former Instituto Nacional de Investigaciones sobre Recursos Bióticos (INIREB) where Mario Ramos supported my interest in ornithology and adopted me into his family so I could stay in Chiapas and study birds in the Selva Lacandona as well as in the Tuxtlas mountains region of Veracruz. After this I joined the Western Foundation of Vertebrate Zoology and assisted Lloyd Kiff in the egg and nest collection (the largest in the world). The Kiff family and my dear friend Sam Sumida helped me to improve my English and encouraged me to attend graduate school. Thanks to them, Mr. Ed Harrison, Mike Collopy, and John Robison I came to the University of Florida. Here I worked hard for my Master of Science and Ph.D., met many colleagues from around the world, learned statistics and experimental design of field projects, and met Holly Payne.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Michael P. Moulton

Michael Moulton, Chair
Assistant Professor of
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Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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